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MORPHOLOGY-INFERRED
PHYLOGENY AND A REVISION
OF THE GENUS *EMMOTUM*
(ICACINACEAE)¹

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ABSTRACT

Emmotum Desv. ex Ham. is a Neotropical, primarily Amazonian and Guayanan genus (Icacinaceae) of 13 tree or shrub species, including a new species here described from Amazonas, Brazil, *E. amazonicum* Duno & Carnevali. A cladistic analysis of the 18 taxa of Icacinaceae including 13 of *Emmotum* was carried out using 41 morphological characters. The single most parsimonious tree shows *Emmotum* as a monophyletic group, strongly supported by nine synapomorphies, with *Poraqueiba* Aubl. as the sister group. In addition, two main groups are identified within *Emmotum*. These two groups laxly correspond with the 1872 classification of Engler: *Emmotum* sect. *Brevistyla* Engl. and *Emmotum* sect. *Longistyla* Engl. (= section *Emmotum*). The genus *Pogopetalum* Benth., synonymous within *Emmotum*, is lectotypified by *P. orbiculatum* Benth. (= *E. orbiculatum* (Benth.) Miers). We present a revision of *Emmotum* with information about nomenclature, distribution, ecology, local names, and uses.

Key words: *Emmotum*, Icacinaceae, IUCN Red List, Neotropics, *Pogopetalum*.

Emmotum Desv. ex Ham. is the largest genus of Icacinaceae in the New World. It encompasses 13 exclusively Neotropical species found from northern South America to south-central Brazil and Bolivia. Plants of *Emmotum* are shrubs or trees; the inflorescence is a short panicle, the inner surface of the petals has a conspicuous indument, the ovary is 3-locular (a feature unique in the

family), and the fruits are small with a slightly depressed apex.

Emmotum, a name proposed by A. N. Desvaux, was first described by Hamilton (1825). A few years later, Bentham (1841) described *Pogopetalum* Benth., including the two species *P. acuminatum* Benth. and *P. nitens* Benth. He did not make reference to *Emmotum* or to any other genera of the Olacineae.

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Miers (1852) later described *E. affine* Miers and *E. glabrum* Benth. ex Miers and transferred Bentham's species of *Pogopetalum* to *Emmotum*.

Engler (1872) was the first to propose an infrageneric classification in *Emmotum* with two sections based on attributes of the trichomes on petals, stamens, and ovary. Section *Longistyla* Engl. (= *Emmotum*) was defined by Engler based on the following characters: petals adaxially with red trichomes covering the whole surface, filament of the stamen with the base dilated and the apex attenuate, anthers oblong-ovate with a terete connective, and the style longer than the ovary, whereas section *Brevistyla* Engl. has petals with trichomes at the base and apex, filaments of the stamens with the base and the apex dilated, anthers oblong-linear with the connective fleshy subtetragonous, and the style shorter than the ovary. Engler included *E. glabrum* in his section *Brevistyla* based on a plate published by Miers (1851–1861). This plate, which shows a plant with a short style and stamen with an anther as long as the filament, is more correctly referable to *E. nitens* (Benth.) Miers, and it is this species that is selected as lectotype for section *Brevistyla* (Duno et al., 2007). Engler further assigned *E. orbiculatum* (Benth.) Miers, a species with a short style of less than 0.5 mm long, to section *Longistyla*. Thus, some species assignments were inconsistent with the attributes proposed by Engler to define his sections.

Van Tieghem (1897) described the family Emmotaceae, which he placed close to Icacinaceae, and included the two genera *Emmotum* and *Pogopetalum*. Sleumer (1940) followed Engler's infrageneric division of *Emmotum*, but elevated sections to subgenera. The most complete treatment of *Emmotum* thus far was published by Howard (1942a), in which he proposed four additional species: *E. nudum* R. A. Howard, *E. conjunctum* R. A. Howard, *E. floribundum* R. A. Howard, and *E. fulvum* R. A. Howard. Howard correctly transferred *E. glabrum* to subgenus *Euemmotum* Sleumer, which laxly corresponded to Engler's section *Longistyla*. Howard therefore concluded that the monotypic subgenus *Brevistyla* was of little use and proposed to abandon the infrageneric classification. He was probably unaware that *E. orbiculatum* was better referred to section *Brevistyla*, thus making this bispecific. There are also a few regional treatments of *Emmotum* (Engler, 1872; Carvalho et al., 1973; de Roon, 1994; Howard & Duno de Stefano, 1999), most of which closely followed Howard's (1942a) classification scheme.

Kårehed (2001), using several molecular markers (*ndhF*, *rbcL*, *atpB*, and 18S ribosomal DNA [rDNA]), along with morphological and anatomical evidence,

investigated the relationships of Icacinaceae within the Euasteridae I, including a large number of the genera traditionally included within that family. His results conclusively demonstrated that Icacinaceae are polyphyletic with genera scattered across several families and orders. The analyses identified two major clades within a narrowed circumscription of Icacinaceae, now included within the Garryales, in the Asteridae clade (Angiosperm Phylogeny Group, 2009). These were the *Icacina* A. Juss. group, composed mainly of pantropical lianas, and the *Emmotum* group, composed of mostly Neotropical trees, with the exception of *Platea* Blume, a genus with five Asiatic species.

Here we present the results of a cladistic analysis based on morphological characters that address the following questions. (1) Is the genus *Emmotum* monophyletic? (2) If so, what are its synapomorphies and other delimiting characters? (3) What is the position of the genus relative to other Neotropical genera of the *Emmotum* group? (4) What are the phylogenetic relationships among species of *Emmotum*, especially in the context of the infrageneric classification proposed by Engler (1872)?

MATERIALS AND METHODS

TAXON ANALYSIS

As a result of the taxonomic work of this investigation, 13 species of the genus *Emmotum* are recognized and included as terminal taxa in the ingroup. There are no previous studies exploring the monophyly of *Emmotum*. As mentioned, Kårehed (2001) found the family Icacinaceae not to be monophyletic, and its circumscription was narrowed to include two main groups: the *Icacina* group and the *Emmotum* group. We chose members of this first group as outgroups: *Oecopetalum mexicanum* Greenm. & C. H. Thoms., *Ottoschulzia cubensis* (C. Wright ex Griseb.) Urb., *Poraqueiba paraensis* Ducke, and *P. sericea* Tul. In Kårehed's (2001) study, *Poraqueiba* Aubl. was sister to *Emmotum*, thus supporting the inclusion of this genus as a member of the outgroup. The genera *Oecopetalum* Greenm. & C. H. Thoms. and *Ottoschulzia* Urb. have been mentioned as morphologically and anatomically related to *Emmotum* and *Poraqueiba* (Howard, 1942a, 1942b). The more distantly related Neotropical species *Calatola costaricensis* Standl., a member of the *Emmotum* clade, was used to root the tree. This taxon is characterized by the autapomorphies of dioecious plants, with 4-merous, unisexual flowers (vs. monoecious plants, with 5-merous, bisexual flowers).

Table 1. Continuous morphological characters in the cladistic analysis of *Emmotum*. Letters a, b, c, and d correspond to character states 0, 1, 2, and 3, respectively.

	Character 5, petiole length (cm)	Character 6, lamina length (cm)	Character 9,		Character 15, no. of flowers	Character 24, filament length (mm)	Character 28,		Character 32, style length (mm)	Character 37, fruit size (cm)
			no. of secondary veins				anther:filament length ratio			
<i>Calatola costaricensis</i>	2–5, b	10–25, b	6 to 8, b		> 50, c	0, a	5:1, a		0, a	4–7, a
<i>Ottoschulzia cubensis</i>	0.4–0.8, a	2.5–5, a	5 to 8, b		1 to 3, a	ca. 2.5, b	1:1, b		5–5.5, d	2–2.5, a
<i>Oecopetalum mexicanum</i>	(0.7–)1–2, b	10–25, b	5 to 7, b		> 50, c	2.2–3, b	1:1, b		ca. 5, d	1.8–2.2, a
<i>Poraqueiba paraensis</i>	1.5–2, b	10–18, b	4 to 6, b		10 to 20, b	ca. 3.5, b	1:2, c		ca. 0.5, b	5–7, b
<i>P. sericea</i>	2–4, b	15–25, b	7 to 9, b		10 to 20, b	ca. 3.5, b	1:2, c		ca. 0.5, b	6.5–7.5, b
<i>Emmotum acuminatum</i>	(1–)1.5–2, b	8–16, b	6 to 9, b		10 to 20, b	ca. 4, b	1:4, d		3–4, c	ca. 1.5, b
<i>E. affine</i>	(1–)1.5–2.5, b	7–12, b	6 to 9, b		10 to 20, b	3.5–4, b	1:4, d		2.5–3, c	ca. 1.5, b
<i>E. amazonicum</i>	1–1.5, b	7–10, b	11 to 14, b		10 to 20, b	ca. 2, a	1:1, b		ca. 0.5, b	ca. 1.5, b
<i>E. celiae</i>	0.4–0.8, a	2–5, a	2 to 3, a		10 to 20, b	2.2–3, b	1:4, d		3–4, c	ca. 0.8, b
<i>E. conjunctum</i>	(1–)1.2–2, b	8–12, b	9 to 13, b		10 to 20, b	4–4.5, b	1:4, d		3–4, c	ca. 1.5, b
<i>E. fagifolium</i>	1–2, b	6.5–18, b	6 to 9, b		10 to 20, b	3.5–4, b	1:4, d		2.5–3.5, c	ca. 1.5, b
<i>E. floribundum</i>	1.5–2.5, b	8–14, b	8 to 11, b		10 to 20, b	4.5–5, b	1:4, d		3.5–4, c	ca. 1.5, b
<i>E. fulvum</i>	ca. 1.5, b	10–16, b	6 to 9, b		10 to 20, b	4.5–5, b	1:4, d		3–3.5, c	ca. 1.5, b
<i>E. glabrum</i>	0.5–0.8(–1), a	5–13, a	2 to 5, a		10 to 20, b	2.8–3, c	1:4, d		2.5–3, c	ca. 1.5, b
<i>E. harleyi</i>	1.3–1.5, b	5–10, a	9 to 11, b		10 to 20, b	1.5–1.8, a	1:1, b		ca. 0.5, b	1–1.2, b
<i>E. nitens</i>	1.5–2.5, b	(5–)6–12, b	6 to 8, b		10 to 20, b	1.5–2, a	1:1, b		ca. 0.5, b	ca. 1.5, b
<i>E. orbiculatum</i>	1–2, b	10–20, b	8 to 9, b		10 to 20, b	ca. 2, a	1:1, b		ca. 0.5, b	ca. 1.5, b
<i>E. yapacanum</i>	0.5–0.8, a	6–7, a	2 to 3, a		5 to 10, b	2.5–4, c	1:4, d		2.5–3, c	ca. 1.5, b

Table 2. Data matrix used in the cladistic analysis of *Emmotum*.

<i>Calatola costaricensis</i>	021011x0110000210?120?3003?03300001000020
<i>Ottoschulzia cubensis</i>	000000200001110001000?1201112303000011000
<i>Oecopetalum mexicanum</i>	001011001101112001100?1201112303000001200
<i>Poraqueiba paraensis</i>	011111001101211001100?0200010001000000000
<i>P. sericea</i>	011111001101211001100?0200010001000000000
<i>Emmotum acuminatum</i>	012111x0110121101011102212123212110111111
<i>E. affine</i>	x1211101110121101011102202123202011111111
<i>E. amazonicum</i>	01211121110121101011112102214101010111111
<i>E. celiae</i>	11210020000121101011102202123202011111111
<i>E. conjunctum</i>	x12111x1111121101011102202123202011111111
<i>E. fagifolium</i>	012111x0110121101011102202123202011111111
<i>E. floribundum</i>	01211121111121101011102212123212110111111
<i>E. fulvum</i>	012111x1111121101011102202123202011111111
<i>E. glabrum</i>	x1210010000121101011102202123202011111111
<i>E. harleyi</i>	01211101111121101011112102214101010111111
<i>E. nitens</i>	01211101111121101011112102214101011111111
<i>E. orbiculatum</i>	01211121111121101011112102214101011111111
<i>E. yapacanum</i>	11210010000121101011102202123202011111111

x = polymorphic character 0,1; ? = not applicable character.

SAMPLING

A morphological data matrix was obtained after careful examination of more than 200 herbarium specimens of *Emmotum* and the outgroup taxa from the following 25 herbaria: A, AAU, BM, CAS, ECON, F, G, GH, INPA, K, LBP, MA, MER, MEXU, MICH, MO, MY, NY, PMA, PORT, S, SCZ, US, VEN, and XAL. Specimens examined included the types of all described terminal taxa.

CHARACTERS AND CODING

Forty-one morphological characters were obtained from general vegetative and reproductive morphology. Most characters were discrete, but a few were continuous, namely petiole length (character 5), lamina length (character 6), number of secondary veins (character 9), number of flowers (character 15), length of the filament (character 24), anther:filament length ratio (character 28), style length (character 32), and fruit size (character 37), which were transformed (binary or multistate) by identification of conspicuous gaps in the interspecific variation of the taxa (Table 1). All characters used in the analysis are listed and described in Appendix 1, and the data matrix is presented in Table 2. All characters were similarly weighted, and multistate characters were considered as unordered (nonadditive, Fitch parsimony [Fitch, 1971]).

Terminology follows the Systematic Association Committee for Descriptive Biological Terminology (1962) for leaf shape and apex (characters 7, 23, 26, and 36). The trichome terminology used in this study (characters 3, 4, and 21) has been compared with a major survey of Icacinaceae (Heintzelman & Howard,

1948). There is a wealth of anatomical and pollen information for the family (see Kårehed, 2001, for bibliography), but most of these characters turned out to be noninformative in the context of the ingroup-outgroup relationships herein.

PHYLOGENETIC ANALYSES

The phylogenetic analyses were performed with the program NONA (Goloboff, 1993) in conjunction with a WinClada shell (Nixon, 2002). The parsimony ratchet algorithm (Nixon, 1999) was implemented to optimize the parsimony search with the following settings: number of iterations/repetitions = 200 and number of trees to hold/iteration = 1. Support for the clades recovered from the analyses was estimated with the use of 1000 jackknife iterations (JK) and the following search parameters: 30 search replicates (mult*30), three starting trees per replication (hold/3), and maximum number of trees set to 25,000. Additional support for these clades was evaluated with the use of the Bremer index or Bremer decay index (Bremer, 1988) with the following parameters: 20,000 trees as maximum number held in memory (h 20000), the longest of them 10 steps longer than the most parsimonious trees (with the implementation of the bootstrap [BS] 10 command).

RESULTS

CLADISTIC ANALYSIS

Of the 41 characters originally explored, the number of flower parts (character 12), sexuality of the flower (character 14), sepal aestivation (character 16), and

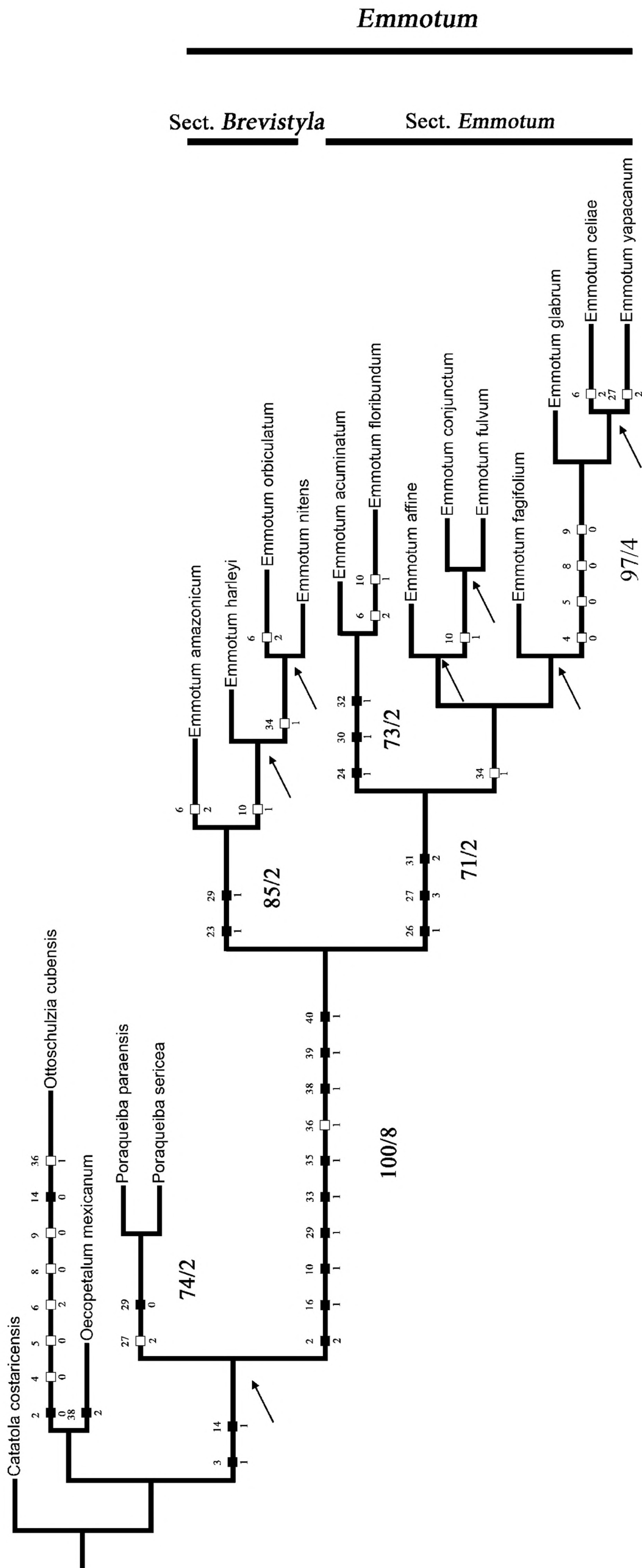


Figure 1. The cladistic analysis resulted in one most parsimonious tree (MPT) with 77 steps, a consistency index (CI) of 0.76, and a retention index (RI) of 0.85. This tree unambiguously identifies *Emmotum* as a monophyletic group. *Emmotum* and *Emmotum* sect. *Brevistyla* show a moderate support (jackknife 71% and 85%). The black squares represent synapomorphies and white squares represent homoplasies (reversions and parallelisms); the numbers above the squares represent the characters and the numbers below the squares represent the Bremer index or Bremer decay index. The black arrows show clades without support.

petal connation (character 19) were not phylogenetically informative (12% of the original data). These characters were thus excluded from consecutive analyses. The cladistic analysis resulted in a single most parsimonious tree (MPT) of 77 steps, with a consistency index (CI) of 0.76 and a retention index (RI) of 0.85. The single MPT obtained (Fig. 1) unambiguously identifies *Emmotum* as a highly supported (JK = 100%, BS = 8) monophyletic group with nine synapomorphies and *Poraqueiba* as the sister taxon, with which it shares two synapomorphies.

DISCUSSION

ROBUSTNESS OF THE PHYLOGENETIC HYPOTHESIS

Similar morphological analyses at the species level show a similar number of morphological and/or anatomical informative characters, e.g., *Asarum* L. with 32 taxa (ingroup) and 37 characters (Kelly, 1997) and *Monsonia* L. with 25 taxa (ingroup) and 20 characters (Aldasoro et al., 2001). Some other analyses, with more characters, attempt to resolve relationships at the species and generic levels (e.g., Schulman & Hyvönen, 2003, for the genus *Adelobotrys* DC., Melastomataceae). In this case, the data matrix included up to 117 morphological characters (91 informative). This high number of characters is due to the inclusion of a large number of outgroup taxa, up to 10 species in seven different genera, thus increasing the number of informative characters. The inclusion in our analysis of some lianoid genera such as *Casimirella* Hassl., *Leretia* Vell., or *Mappia* Jacq. could result in the addition of new morphological, anatomical, and palynological informative characters. However, the inclusion of these characters, although providing better resolution at the base of the tree, would increase neither the resolution nor the support to the taxa and clades in the ingroup, which is our main focus. It is unlikely that many additional, informative macromorphological characters could be discovered, rendering the search of micromorphological or molecular data necessary to provide further resolution of species relationships.

The CI of the single MPT, 0.76, falls near the higher end of the range normally obtained in similar, morphology-based analyses (Sanderson & Donoghue, 1989). These ranges of the CI indicate a moderate level of homoplasy. The topology of the consensus tree, and character states with unambiguous optimization supporting relevant clades, are described below.

MONOPHYLY OF *EMMOTUM*

At the base of the single MPT, the clade formed by *Ottoschulzia cubensis* and *Oecopetalum mexicanum*

appears as sister to a clade comprising the genera *Poraqueiba* and *Emmotum*. *Ottoschulzia cubensis* shows two autapomorphies: malpighiaceae hairs with unequal arms (character 3) and inflorescences with one to three flowers (character 15). There is also one autapomorphy for the genus that appears as non-informative: the petal joined at the base (character 19). For *Ottoschulzia* there are also other vegetative and floral character states that represent reversions (e.g., a reduction in the size of the petiole [character 5] and the lamina [character 6], type of apex [character 7], few, nonconspicuous secondary veins [characters 9 and 10], and small fruits [character 37]). On the other hand, the genus *Oecopetalum* shows one autapomorphy, fruits with an acute apex (character 39), but this genus also shows several other unique floral characters that were not included in the analysis (e.g., persistent calyx, petals with prominent midrib [unlike those of *Poraqueiba*], and the anthers with lateral dehiscence). The inclusion of these characters (see Greenman & Thompson, 1914; Howard, 1942b) would not affect the topology, resolution, or support for the tree because they are autapomorphic.

The status of *Poraqueiba* as sister taxon to *Emmotum*, as inferred by Kårehed (2001), is supported by our results. Both genera have Amazonian or Guayanan distributions, while the other outgroups have Antillean and Central American distributions; two synapomorphies support this clade, namely articulated hairs (character 4) and number of flowers (character 15).

PHYLOGENY OF *EMMOTUM*

Emmotum is easily diagnosable and strongly supported by nine synapomorphies: red pigmentation of tissues upon pickling (character 2); white flowers (character 17); slightly developed petal texture (character 20); petals with cylindrical hairs (character 21); multilocular ovary (character 34); fruits small, less than 1.5 cm long (character 37), and with the apex shortly mucronate (character 39); slightly developed endocarp (ch. 40), and seed with a relatively large embryo (character 41).

Within *Emmotum*, two clades are identified. These clades correspond to Engler's (1872) sections, later reprised as Sleumer's (1940) subgenera. The first clade corresponds to *Emmotum* sect. *Brevistyla* (JK = 85%, BS = 2) and consists of four species found only south of the equator, principally in Brazil. *Emmotum orbiculatum* is from the Brazilian states of Amazonas and Pará, representing the northernmost member of this clade. *Emmotum nitens* grows in the cerrado of Brazil to Minas Gerais and Bolivia and is the most

austral taxon of the clade. Two sets of populations formerly referred to *E. nitens* deserve recognition as separate species—*E. amazonicum* Duno & Carnevali, described below, is restricted to the state of Amazonas, Brazil, where it is partially sympatric with *E. orbiculatum*, while *E. harleyi* Duno is restricted to the Chapada Diamantina in Bahia, Brazil (Duno et al., 2007). This Brazilian clade is characterized by two synapomorphies: filaments 1.5–2 mm long (character 24) and the stamen connective slightly developed (character 30). These four taxa feature discontinuous indument with only two clusters of hairs (character 22), one at the base and another at the apex of the adaxial surface, but the character is not applicable to any member of the outgroup.

The second clade corresponds to *Emmotum* sect. *Emmotum* and includes nine species (JK = 71%, BS = 2). The clade is characterized by three synapomorphies: the apex of the filament dilated (character 27), the anther three or four times longer than the filament (character 28), and the style 2.5–4 mm long (character 32). As here circumscribed, this clade corresponds to those species with densely lanate petals, stamens with filaments dilated at the base and attenuate at the apex, and the anthers ovate. This second clade includes the generitype, *E. fagifolium* Desv. ex Ham.

Within *Emmotum* sect. *Emmotum*, a clade made up of *E. acuminatum* (Benth.) Miers and *E. floribundum* (JK = 73%, BS = 2) is sister to the rest of the taxa. They have three synapomorphies: a dorsifixed anther (character 25), a diminute ring of tissue around the base of the ovary (character 31), and lateral styles (character 33). Another clade contains two subclades, one containing *E. conjunctum* R. A. Howard and *E. fulvum*, and another containing the other five species. On the other hand, *E. affine* is sister to *E. conjunctum* and *E. fulvum*. These two taxa are not supported by any synapomorphy but by one character state reversion, a lamina with caducous pubescence (character 11). Both species occur on sandstone-derived substrates of the Guayana Region, but *E. fulvum* inhabits low, medium to tall forests on tepui slopes between 850 and 1700 m, while *E. conjunctum* grows in several kinds of savanna associations and forests, between 300 and 1400 m. *Emmotum fagifolium* is the sister taxon of a clade including three Guayanan species, *E. glabrum*, *E. celiae* R. A. Howard, and *E. yapacanum* R. A. Howard (JK = 97%, BS = 4) with four reversions: short petioles, 0.4–0.8 cm long (character 5), a small lamina, 2–5 cm long

(character 6), lamina with only two or three pairs of secondary veins (character 9), and inconspicuous secondary veins (character 10).

EVOLUTION OF SELECTED CHARACTERS

Petals

In the genus *Poraqueiba* the petals are fleshy and glabrous with two internal furrows separated by a usually well-developed median ridge. *Emmotum*, on the other hand, has petals slightly fleshy (character 20), densely indumented with cylindrical hairs (character 21), and lacking internal furrows and ridge.

Stamens

In the *Emmotum* group of the Icacinaceae, the transformation of the stamens is one of the most relevant evolutionary trends. In *Poraqueiba*, the stamens have fleshy, thickened filaments and anthers with wide, elongated connectives. An examination of the evolution of the features associated with the androecium in *Emmotum* indicates a trend toward an elongation of these parts. In *Emmotum* sect. *Brevistyla*, the stamens are similar to those of *Poraqueiba* but with thinner connectives, anthers, and filaments. In *Emmotum* sect. *Emmotum*, the stamens become thin and longer, and the connective becomes ovate with no prolongation. The analysis shows that the different characters associated with the stamen morphology are involved in the topology of the single MPT. For example, *Poraqueiba* is supported by two characters (27 and 29) from stamen morphology and *Emmotum* sect. *Emmotum* is also defined by a synapomorphy associated with these characters (28). Also, in *Emmotum* sect. *Emmotum*, another clade (*E. acuminatum* and *E. floribundum*) is supported by a stamen character (25); in this case, the anthers become dorsifixed. We believe many of these stamen's characters are strongly correlated, e.g., relative size of the filament and the anther, shape of the anther, and shape and prolongation of the connective.

Ovary

One of the most important characteristics of the genus *Emmotum* is the multilocular ovary (character 34), which is not found in any other Icacinaceae. Another important character is the length of the style (character 32). There is a trend toward an elongation of the style in the evolution of the *Emmotum* group. *Poraqueiba* has an inconspicuous style; in *Emmotum* sect. *Brevistyla*, the style is slightly longer, while it is longest in *Emmotum* sect.

Emmotum. The clade *E. acuminatum*–*E. floribundum* is characterized by a shift in the style from a central to a lateral position (character 33) while its surface becomes glabrous, a reversal to a more ancestral character state found in the other genera of the *Calatola*–*Oecopetalum*–*Poraqueiba* clade (although glabrous in *Calatola* Standl.).

Vegetative characters

The most obvious vegetative changes occur in the clade composed of *Emmotum celiae*, *E. glabrum*, and *E. yapacanum*. In this group, and according to our results, at least five evolutionary changes in the leaves have occurred. These changes involve a decrease in petiole length (character 5) and an overall reduction in the size of the lamina (character 6). Furthermore, the number of secondary veins is drastically reduced (character 9) and poorly developed (character 10). It remains to be addressed whether these changes are adaptations to the more restrictive conditions of the tepui summit habitats.

TAXONOMIC SYNOPSIS

I. *Emmotum* Desv. ex Ham., Prodr. Pl. Ind. Occid. (Hamilton): 29. 1825. TYPE: *Emmotum fagifolium* Desv. ex Ham.

Trees or shrubs with decumbent branches, up to 5–20(–30) m high, generally all parts pubescent, the indument gray to ferruginous or golden, articulated, erect, rarely undulate, variable in length, generally appressed. *Leaves* alternate, coriaceous or subcoriaceous, generally bicolored, green to golden on the abaxial surface and dark green and lustrous on the adaxial surface; lamina narrowly ovate, ovate, narrowly elliptic, elliptic to nearly orbicular, apex acuminate, acute, or mucronate, rarely retuse, base acute, obtuse, or attenuate, margin entire, slightly revolute; secondary veins in 2 to 14 pairs, variously developed, alternate, free near the margins or joined together in a series of marginal loops; abaxial surface glabrous, sericeous to velvety, rarely tomentose, hairs caducous to persistent; petiole to 2.5 cm, canaliculate, a nitid line of abscission at the base, puberulent, sericeous, or velvety, rarely glabrescent. *Inflorescence* axillary, paniculate, to 5 cm, pedicels short, articulated apically, sericeous or densely sericeous. Bracts triangular or widely triangular, slightly concave, sericeous outside, glabrous within. *Flowers* pentamerous, actinomorphic, bisexual, hypogynous, fragrant; bracteoles 1 or 2 per flower,

subtriangular to triangular, concave, sericeous outside and glabrous within; pedicels to 3 mm, sericeous to densely sericeous; *calyx* campanulate, fleshy, lobes broadly triangular to triangular, sericeous outside, glabrous within, apex acute, margin entire; *corolla* with the petals free, white, obovate, oblong, or narrowly oblong, sericeous outside, rarely glabrous, densely lanate within, sometimes 2 clusters of trichomes at the base and the apex; margin entire; apex acute, reflexed; main vein patent within; *stamens* with fleshy, flattened, erect, glabrous filaments, base dilated, apex dilated or attenuate; anthers tetragonous or cordate, attached basally, rarely dorsally, longitudinally dehiscent; connective ovate or elliptic, sometimes prolonged beyond anther thecae; *gynoeceum* surrounded by a well-developed ring of glabrous tissue at the base of the ovary, a true disk absent; *pistil* with the ovary globose, hirsute or glabrous, 2- or 3-locular; style central, sometimes eccentric, long, rarely very short; stigma capitate, rarely 3-lobed. *Fruits* subglobose, exocarp very thin, green when immature and yellow to black when mature; mesocarp thin; endocarp hard, with 3 poorly developed ribs; seeds in general 1, rarely 2 to 3.

Etymology. Miers (1852) mentioned that he did not know the origin of the name, but suggested that it comes from the Greek ευ (prefix meaning “well”) and μωτος (linen cloth), in reference to the densely lanate inner surface of the petals.

Discussion. Van Tieghem’s (1897) lectotypification of the genus *Pogopetalum* (published in 1841) with *P. nitens*, described in 1843, is untenable because this species is not part of the protologue of the genus (McNeill et al., 2006: Art. 9.10, 10.1). Bentham originally cited two species for the genus in 1839: *P. orbiculatum* and *P. acuminatum*. The generic diagnosis of *Pogopetalum* features characters attributable to both species, but the plate (tab. XLII) can be unambiguously referred to *P. orbiculatum*, which was the only member of *Emmotum* sect. *Brevistyla*, based on its short style and characters of the stamens similar to those of other members of *Emmotum* sect. *Brevistyla*.

KEY TO THE SECTIONS OF *EMMOTUM*

- 1a. Filaments basally dilated, apically attenuated; anthers oblong-linear; connective ovate; ovary with a long style, 2–5 mm long *Emmotum* sect. *Emmotum*
- 1b. Filaments dilated both basally and apically; anthers oblong; connective elliptic and prolonged; ovary with a short style, less than 0.5 mm long *Emmotum* sect. *Brevistyla*

KEY TO THE SPECIES OF *EMMOTUM*

- 1a. Lamina with secondary veins poorly developed, with 2 to 5 pairs of veins; mostly glabrous when mature.
 - 2a. Lamina $2-5 \times 1.1-3$ cm, obovate, the apex acute or rounded, slightly mucronate, the base attenuate, 2 or 3 pairs of secondary veins *E. celiae*
 - 2b. Lamina $5-13 \times 3-4.5$ cm, ovate or elliptic, the apex short- or long-acuminate, the base acute-attenuate, 2 to 5 pairs of secondary veins.
 - 3a. Peduncle of the inflorescence less than 1.5 cm long *E. glabrum*
 - 3b. Peduncle of the inflorescence ca. 3 cm long *E. yapacanum*
- 1b. Lamina with secondary veins well developed or covered with a dense indument, with 5 to 14 pairs of veins; pubescent or glabrous when mature.
 - 4a. Petals adaxially with only clusters of hairs at the base and the apex, more rarely the hairs laxly continuous from base to apex; style less than 1 mm long (section *Brevistyla*).
 - 5a. Lamina densely tomentose on the abaxial surface; petals sparsely lanate adaxially along the main vein; ovary glabrous *E. harleyi*
 - 5b. Lamina with indument of variable density on the abaxial surface; petals with clusters of trichomes at the base and the apex alone; ovary hirsute, rarely glabrous.
 - 6a. Lamina broadly elliptic to suborbicular *E. orbiculatum*
 - 6b. Lamina narrowly ovate to elliptic-oblong.
 - 7a. Lamina elliptic to elliptic-oblong, 11 to 14 pairs of secondary veins, dark brown, abaxial surface puberulent, brown-yellow; ovary glabrous *E. amazonicum*
 - 7b. Lamina narrowly ovate, ovate, elliptic to elliptic-oblong, fewer than 9 pairs of secondary veins, dark green to dark yellow, occasionally dark brown, abaxial surface villose, yellow, occasionally brown-yellow; ovary hirsute *E. nitens*
 - 4b. Petals densely lanate adaxially; style long, 2.5–4 mm long.
 - 8a. Ovary hairy, the style central.
 - 9a. Lamina bicolored, abaxial surface densely velvety with long, slightly undulate trichomes ... *E. fulvum*
 - 9b. Lamina concolorous, abaxial surface glabrous, sericeous, or tomentose.
 - 10a. Lamina elliptic, $7-12 \times 3-7$ cm; 6 to 9 pairs of secondary veins *E. affine*
 - 10b. Lamina oblong, elliptic, or ovate, $6.5-18 \times 3-8$ cm; 7 to 13 pairs of secondary veins.
 - 11a. Abaxial surface of the lamina slightly pubescent with very short trichomes; the secondary veins free at the end, 9 to 13 pairs of secondary veins *E. conjunctum*
 - 11b. Abaxial surface of the lamina almost glabrous; the secondary veins joined together in a series of marginal loops, 6 to 9 pairs of secondary veins *E. fagifolium*
 - 8b. Ovary glabrous, the style lateral.
 - 12a. Lamina ovate or oblong, drying dark brown, chestnut, or tan abaxially; secondary veins 6 to 9 pairs, abaxial surface glabrous; the apex acuminate *E. acuminatum*
 - 12b. Lamina elliptic or orbiculate, drying green-brown; secondary veins 8 to 11 pairs, abaxial surface sericeous; the apex acute or mucronate *E. floribundum*

1a. *Emmotum* Desv. ex Ham. sect. *Emmotum*.
Emmotum sect. *Longistyla* Engl., Fl. Bras. (Martius) 12(2): 44. 1872. *Emmotum* subg. *Euemmotum* Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 15: 233. 1940. TYPE: *Emmotum fagifolium* Desv. ex Ham.

Emmotum sect. *Emmotum* is characterized by the flowers with the petals densely lanate within; stamens with the filament dilated at the base, but the apex attenuate; the anthers oblong to linear; and the ovary with a long style, exceeding 1 mm, that is centric or eccentric in position. This section includes the following nine species: *E. acuminatum*, *E. affine*, *E. celiae*, *E. conjunctum*, *E. fagifolium*, *E. floribundum*, *E. fulvum*, *E. glabrum*, and *E. yapacanum*.

1. *Emmotum acuminatum* (Benth.) Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 178. 1852.
 Basionym: *Pogopetalum acuminatum* Benth., Proc. Linn. Soc. London 1(10): 88. 1841 [6

Apr. 1841]. TYPE: Brazil. Amazonas: growing on the high banks of the Rio Negro, R. Schomburk 970a (holotype, K!; isotypes, F!, G!, K!, P not seen, US!).

Emmotum nudum R. A. Howard, J. Arnold Arbor. 23: 485, tab. I. 1942. TYPE: Brazil. Pará: Faro, “in campis arenosis loco Tigre,” 31 Dec. 1929, A. Ducke 11367 (holotype, US!; isotypes, K!, U not seen).

Shrubs or trees, to 20 m. *Leaves* coriaceous, not bicolored, dark brown-green on both surfaces; lamina $8-16 \times 3-9$ cm, oblong to ovate, rarely elliptic, apex slightly acuminate to acute, base rounded or slightly obtuse, puberulent on the abaxial surface, glabrous on the adaxial surface; secondary veins 6 to 9 pairs, conspicuous; petiole (1–)1.5–2 cm. *Inflorescences* axillary, 1- to 5-floriferous branches, to 3 cm; *calyx* campanulate, sepal lobes ca. 1×0.8 mm, triangular; *corolla* with white petals, $4-5 \times 1.2-1.5$ mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 4–5 mm, filaments ca. 4 mm, slightly swelled; anthers dorsifixed, connective

ovate; *pistils* 5–5.5 mm, ovary glabrous; style 3–4 mm, eccentric. *Fruits* ca. 1.5×1.5 cm (diam.).

Distribution and ecology. *Emmotum acuminatum* is known from Venezuela (Amazonas), Guyana (Cuyuni-Mazaruni), and Brazil (Amazonas, Pará, Rondônia, and Roraima). It grows in forests and savannas at elevations between 50 and 120 m.

Phenology. *Emmotum acuminatum* flowers between October and July and fruits between March and December.

IUCN Red List category. Given its distribution in Amazonian Brazil and the Guianas (Venezuela and Guyana), this species is listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Discussion. In the phylogenetic analysis, *Emmotum acuminatum* is the sister species of *E. floribundum*. Both species share the following synapomorphies: dorsifixed anthers and ovary glabrous with a long, eccentric style. In addition, they grow sympatrically in part of their distribution.

Additional specimens examined. BRAZIL. **Amazonas:** Manaus, Igarapé do Franco, *Chagas* 3578 (A); rio Trombetas, margem direita ao norte da Mineração St. Patricia, campina do Monte Branco, *C. A. Cid Ferreira et al.* 1464 (A, NY); Boca do Río Ararirá, margem direita do rio Negro, *C. A. Cid Ferreira* 9283 (GH, NY); Manaus, loco Cachoeira Grande, *A. Ducke* 376 (A, MO, NY, R); Manaus, Estr. Aleixo, *A. Ducke* 2012 (A, GH, NY, R, US); BR156, betw. Calçoene & Rio Amapá Grande, ca. 35 km S of Calçoene, *B. V. Rabelo et al.* 2994 (A, F, MO, NY, US); Manaus, Igarapé do Parque 10, *Pessoal do CPF* 6158 (A); Secus Rio Negro, inter Barcellos & San Isabel, *R. Spruce* 1969 (NY [photo]); Secus Rio Negro, inter Barcellos & San Isabel, *R. Spruce* 1989 (G, K, MO, US [photo]). **Pará:** Ilha do Marajo, Sitio Campina, on river Pracuuba-mirim, ca. 1 hr. by boat upstream from São Sebastião de Boa Vista, *G. L. Sobel et al.* 4558 (MO). **Rondônia:** Igarapé Preto, *B. G. S. Riberiro* 1085 (A). **Roraima:** Rio Xeriuini, *J. M. Pires et al.* 13994 (A, INPA); Río Branco, margen esquadrada do Paraná do Marará, *M. R. Santos* 141 (NY). GUYANA. **Cuyuni-Mazaruni:** Kukenan River, *Schomburgk* 970 (K [2], F [photo], G, GH, MO [photo], NY [photo], US). VENEZUELA. **Amazonas:** Río Guainía, just S of Maroa, *B. Maguire & J. J. Wurdack* 36439 (A, NY, VEN); along river just above Tamatama, *J. J. Wurdack & L. S. Adderley* 43120 (GH, NY, VEN).

2. *Emmotum affine* Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 180. 1852. TYPE: Brazil. Brasília, s.d., *F. Sellow* s.n. (holotype, K!).

Shrubs and trees, 4–10 m. *Leaves* coriaceous, sharply bicolored, green-grayish on the abaxial surface, dark green and shiny on the adaxial surface;

lamina 7–12 $\times$ 3–7 cm, elliptic to ovate, apex slightly acuminate to acute, base rounded or slightly obtuse, sericeous on the abaxial surface, glabrous on the adaxial surface; secondary veins 6 to 9 pairs, conspicuous; petiole (1–)1.5–2.5 cm. *Inflorescences* axillary, (1)3- to 4(5)-floriferous branches, up to 4 cm. *Flowers* pentamerous; pedicels 3 mm; *calyx* campanulate, sepal lobes ca. 1×0.8 mm, triangular; *corolla* with petals white, 4.5–5 $\times$ 1.2–1.5 mm, narrowly oblongate, densely pilosulose, forming a beard on the adaxial surface; *stamens* 4–4.5 mm, filaments 3.5–4 mm, slightly swelled; anthers basifixed, connective ovate; *pistils* 3.5–4.5 mm, ovary hirsute; style 2.5–3 mm, terminal. *Fruits* ca. 1.5×1.5 cm (diam.).

Distribution and ecology. *Emmotum affine* is endemic to the northeastern coast of Brazil, in Bahia, Espírito Santo, Pernambuco, and Sergipe. It grows in the coastal forest (restinga) in sandy soils between 0 and 50 m elevation.

Phenology. *Emmotum affine* has been collected in flower in October to July and in fruit in December to July.

IUCN Red List category. *Emmotum affine* does have a wide distribution (northeast Brazil). However, it grows in one of the most threatened ecosystems in Brazil, the Mata Atlântica, and it is therefore listed as Vulnerable (VU), according to IUCN Red List criteria (IUCN, 2001).

Discussion. *Emmotum affine* is a shrub or small tree from the Brazilian restinga. In the phylogenetic analysis it emerges as sister species to a clade with two species, *E. conjunctum* and *E. fulvum*. However, from a phenetic point of view it is more similar to *E. fagifolium*. It differs from *E. fagifolium* in its ovate to elliptic lamina (vs. ovate to oblong, sometimes elliptic), apiculate or acute apex (vs. long acuminate to acute), and the sericeous indument on the abaxial surface (vs. glabrous).

Additional specimens examined. BRAZIL. **Bahia:** Marau a Ubaitaba, *J. Almeida & T. S. Santos* 107 (A, NY); Marau, *R. P. Belém & R. S. Pinheiro* 3042 (A [3], NY); Santa Cruz Cabralia, *R. P. Belém & R. S. Pinheiro* 3305 (A [3], NY); Parque Nacional Monte Pascoal, *S. G. da Vinha & T. S. Santos* 968 (A, NY); 65 km NE of Itabuna, at mtn. of Rio de Contas on N bank, opposite Itacaré, *R. M. Harley et al.* 18388 (K, MO); 11 km S of Santa Cruz Cabralia, *R. M. Harley et al.* 17055 (A, NY, US); Copuva, *G. Hatschbach & J. M. Silva* 48754 (MO, US); rd. BA 001, trecho Alcobaça/Prado, a 5 km a NW de Alcobota, *S. A. Mori et al.* 10577 (A, K, NY); Rodovia BR 030, trecho Ubaitaba/Marau, 45–50 km a leste de Ubaita, *S. A. Mori et al.* 11971 (A, NY); rd. BR 500, 18.7 km ao N de Santa Cruz de Cabralia, *S. A.*

Mori et al. 12122 (A, US); BA-099 Estrada do Côco, Guarajuba, Reserva Ecol., *G. C. P. Pinto & H. P. Bautista* 315/83 (K, NY); Barrolândia, Est. Exper. Gregorio Bondar, CEPLAC, 48 km E of BR 101 on rd. to Belmonte, *W. W. Thomas et al.* 9875 (A, NY). **Espírito Santo:** lago do Milho, *A. L. Peixoto et al.* 333 (US); 6 km N of Guarapari, *W. W. Thomas et al.* 6101 (NY). **Pernambuco:** Prazeres, Tapera, *B. Pickel* 3125 (A, F, US). **Sergipe:** ca. 2 km do Distr. Crasto, na estrada Sta. Luzia do Itanhi, *S. C. Sant'Ana et al.* 422 (NY).

- 3. *Emmotum celiae*** R. A. Howard, Mem. New York Bot. Gard. 29: 63, fig. 55. 1978. TYPE: Venezuela. Amazonas: Serranía Yutaje, Río Manapiare, Cerro Yutaje, 21 Feb. 1953, *B. Maguire & C. Maguire* 35351 (holotype, NY!; isotypes, A!, US!). Figure 2.

Shrubs or tree, to 10 m. *Leaves* subcoriaceous, nonbicolored, dark brown-green in both surfaces; lamina 2–5 × 1.1–3 cm, obovate, apex acute or rounded, slightly mucronate, base attenuate, glabrous on both surfaces; secondary veins 2 to 3 pairs, inconspicuous; petiole 0.4–0.8 cm. *Inflorescences* axillary, 1- to 3-floriferous branches, up to 2 cm; peduncle short, no longer than 1 cm. *Flowers* pentamerous; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with the petals white, 3–3.5 × ca. 1 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 3.2–3.5 mm, filaments 2.2–3 mm, slightly swelled; anthers ca. 1.2 mm, basifixed, connective ovate; *pistils* 5–5.5 mm, ovary hirsute; style 3–4 mm, eccentric. *Fruits* ca. 0.8 × 0.6 cm (diam.).

Distribution and ecology. *Emmotum celiae* is endemic to Venezuela, where it has been collected in the northern portion of Amazonas State. It grows in shrublands, low forests, or exposed rocky areas on top of the sandstone plateau of Cerro Yutaje, between 500 and 2000 m elevation.

Phenology. *Emmotum celiae* has been collected in flower and fruit in January and May.

IUCN Red List category. *Emmotum celiae* is only known from a few collections. Without further information, it is best listed as Data Deficient (DD) according to IUCN Red List criteria (IUCN, 2001). However, because it is restricted to isolated sandstone table mountain slopes and summits in a completely inaccessible area, it could alternatively be listed as Least Concern (LC).

Discussion. *Emmotum celiae* emerges as a sister species of *E. yapacanum* in the phylogenetic analysis, but the former has smaller leaves (2–5 cm

vs. 6–7 cm) with an acute or rounded, slightly mucronate apex (vs. long acuminate).

Additional specimens examined. VENEZUELA. **Amazonas:** alrededor de la laguna Asisa, cerro Asisa, Serranía Parú o Asisa, *J. Hoyos & G. Morillo* 88 (CAR, VEN); Serranía Parú, Cerro Parú, just N of valley head of camp, W rim, *R. S. Cowan & J. J. Wurdack* 31059 (A, NY); Serranía Parú, Cerro Parú, *R. S. Cowan & J. J. Wurdack* 31307 (A, K, NY); valley of Río Coro-Coro, W of Serranía de Yutajé, *B. K. Holst & R. L. Liesner* 3273 (A, MO, NY, VEN); valle del Río Coro-Coro, O de la Serranía de Yutajé, *B. K. Holst & R. L. Liesner* 3275, 3325 (MO, VEN); 1 a 2 km al E del Río Coro-Coro, O de la Serranía de Yutajé, *R. L. Liesner & B. K. Holst* 21480 (A, MO, VEN); Serranía Yutajé, Río Manapiare, lefthand Fork Caño Yutajé, *B. J. Maguire & C. K. Maguire* 35275 (MO, NY); Serranía Yutajé, Río Manapiare, Cerro Coro-Coro, *B. J. Maguire & C. K. Maguire* 35430 (A, NY); summit of Cerro Parú, Serranía Parú, *K. C. Phelps & H. Hitchcock* 513 (A).

- 4. *Emmotum conjunctum*** R. A. Howard, J. Arnold Arbor. 23(4): 491, tab. 3. 1942. TYPE: Venezuela. Bolívar [Amazonas]: Mt. Auyan-Tepui, 1100 m, Dec.–Jan. 1937–1938, *G. G. H. Tate* 1354 (holotype, US!; isotype, NY!). Figure 3.

Shrubs or trees, 2–5 m. *Leaves* coriaceous, sharply bicolored, green-brown or green-grayish on the abaxial surface and dark green on the adaxial surface; lamina 8–12 × 3–7 cm, oblong to narrowly oblong, sometimes elliptic to ovate, apex long acuminate to acute, base rounded or slightly obtuse, sericeous on the abaxial surface, glabrous on the adaxial surface; secondary veins 9 to 13 pairs, conspicuous; petiole (1–)1.2–2 mm. *Inflorescences* axillary, 1- to 5-floriferous branches, up to 4 cm. *Flowers* pentamerous; pedicels to 3 mm; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with the petals white, 5–6.5 × 1.5–2 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 5–6.5 mm, filaments 4–4.5 mm, slightly swelled; anthers ca. 1 mm, basifixed, connective ovate; *pistil* 4.5–5.5 mm; ovary hirsute; style 3–4 mm, eccentric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum conjunctum* occurs in Venezuela (Amazonas and Bolívar), Guyana, and probably Roraima State in Brazil. It grows in several kinds of savanna or savanna-like associations and forests, always on sandstone-derived substrates, between 300 and 1400 m elevation.

Phenology. *Emmotum conjunctum* flowers year round and fruits between February and November.

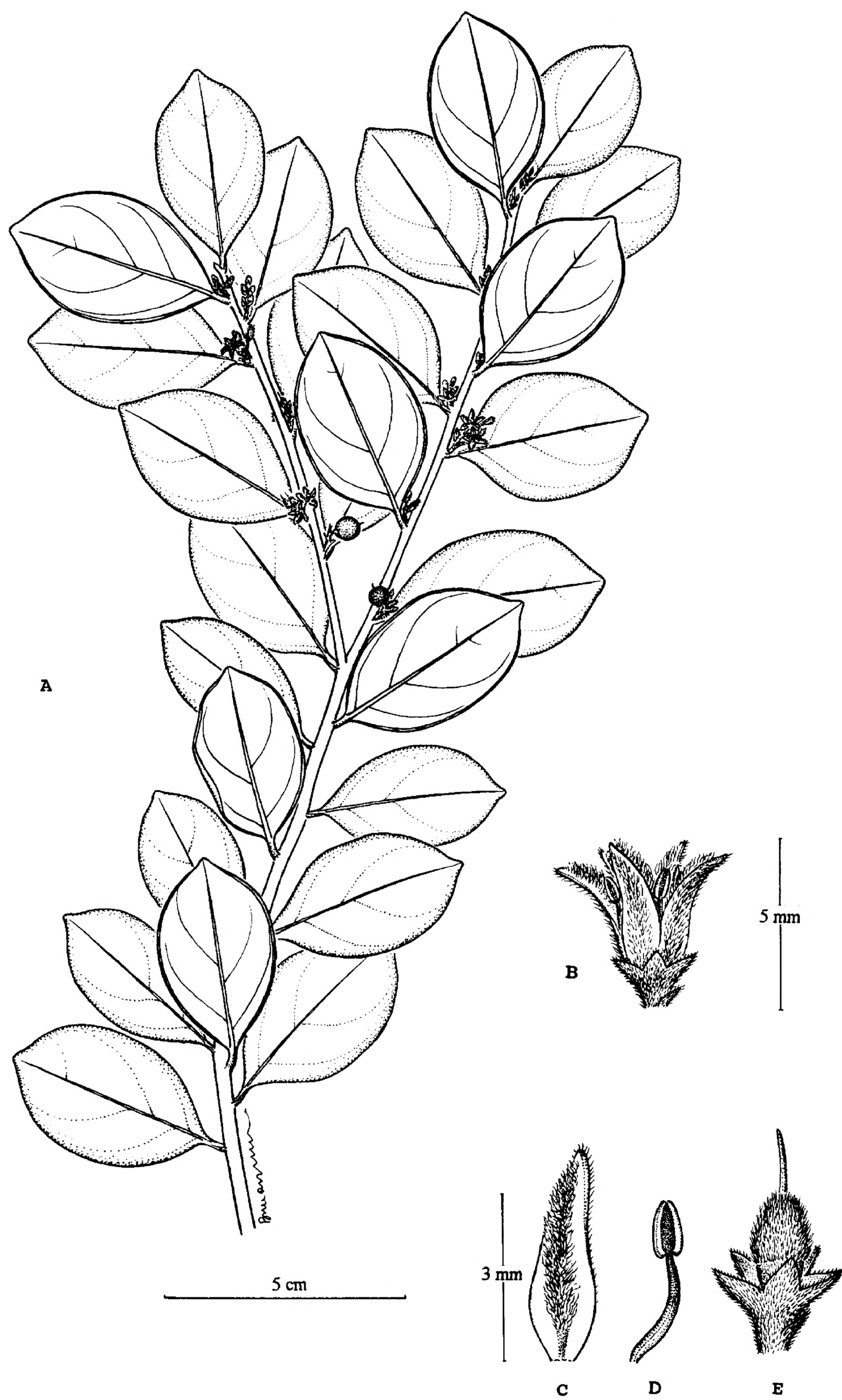


Figure 2. *Emmotum celiae* R. A. Howard. —A. Habit. —B. Flower. —C. Petal inner surface. —D. Stamen. —E. Flower with petals removed and pistil visible. Drawn from *J. Hoyos & G. Morillo 88* (VEN).

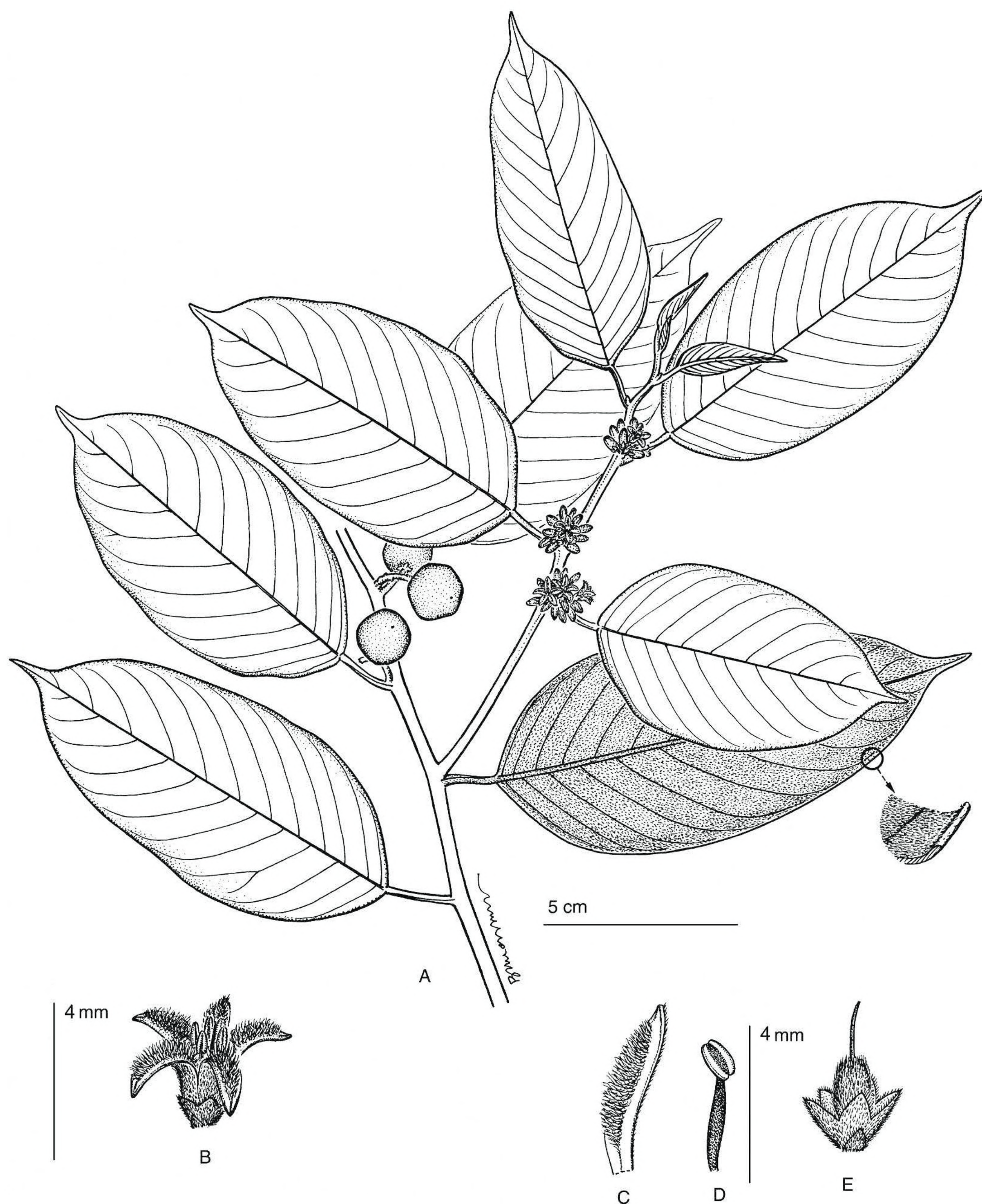


Figure 3. *Emmotum conjunctum* R. A. Howard. —A. Habit. —B. Flower. —C. Petal inner surface. —D. Stamen. —E. Flower with petals removed and pistil visible. Drawn from *Davidse et al.* 4898 (VEN).

IUCN Red List category. *Emmotum conjunctum* has a wide distribution, including areas that are protected and that are not densely populated. It is therefore listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Discussion. *Emmotum conjunctum* is sister to *E. fulvum*, but from a phenetic point of view it is also

similar to *E. fagifolium*. Both species, *E. conjunctum* and *E. fagifolium*, have been treated in divergent ways by different authors. Howard (1942b) hypothesized a relationship of *E. conjunctum* with *E. fulvum* and *E. affine*. On the other hand, Steyermark (1966) considered it conspecific with *E. fagifolium*, but de Roon (1994) kept both species as separate. The type collections of both species show remarkable differences

es, but as more specimens are examined, a close relationship between them becomes evident. However, *E. fagifolium* is limited to the lowlands in the Guianas and Brazil, while *E. conjunctum* is found in the table mountain highlands of Venezuela and Guyana.

Selected specimens examined. VENEZUELA. **Amazonas:** Serranía del Parú (Aroko), *O. Huber* 3623, 3628 (A, NY, VEN); Serranía Yutajé, Río Manapiare, left-hand fork Caño Yutajé, *B. J. Maguire & C. K. Maguire* 35475 (MO). **Bolívar:** La Gran Sabana, ca. Km 202, S of El Dorado along rd. to Santa Elena, Salto Camá, *G. Davidse et al.* 4898 (VEN); O del complejo Guaquinima Tepui, a 42.5 km SE de Entreríos, *G. Aymard & A. Fernández* 7126 (MO, NY); Cerro Arepuchi, Río Caroni, *F. Cardona* 1938 (NY, VEN); Río Icabarú, Alto Caroni, *F. Cardona* 2529 (MO); Gran Sabana along rd. from Icabarú to Santa Elena, 16 km N of Icabarú, *T. B. Croat* 54143 (A, MO, NY); cuesta al N de Kamá, *O. Huber et al.* 7276 (A, NY, VEN); Río Aza medio en el pie de monte septentrional del cerro Zumbador, *O. Huber* 10257 (A, NY, VEN); margen izquierda del Río Trueno alto, aprox. 35 km O del caserio Chiguao, *O. Huber* 10331 (A, NY, VEN); en la región del Río Yuruaní inferior, aprox. 5 km al O de San Ignacio de Yuruaní, *O. Huber* 10455, 10457 (A, NY, VEN); 3 km S of El Pauji, *R. L. Liesner* 19741 (A, MO, VEN); Río Aparamán, affluent of Río Acanán near Yuray-meru rapids, 1.5 km S of SW Amuruay-tepuy, *R. L. Liesner & B. Holst* 20115 (A, MO, NY, VEN); faldas meridionales, vecindad de Guayaraca, en la primera (inferior) meseta (hombrillo) arriba del valle de Kamarata, *J. A. Steyermark* 94204 (A, NY); Gran Sabana, along valley of Río Kamá, S of Río Kamá, at 199 km S of El Dorado on rd. to Santa Elena, *J. A. Steyermark* 111315 (MO, NY, VEN); 8–10 km E de Icabarú, *J. A. Steyermark et al.* 117790 (A, MO, VEN); 7 km NO de Icabarú (fl.), *J. A. Steyermark et al.* 127311 (MO, VEN); río afluyente del Río Uarí, Gran Sabana, *F. Tamayo* 3109 (VEN); Mt. Auyan-Tepui, *G. G. H. Tate* 1354 (NY [2], US).

5. *Emmotum fagifolium* Desv. ex Ham., Prodr. Fl. Ind. Occid. (Hamilton) 29. 1825. TYPE: French Guiana, s.d., *N. A. Desvaux s.n.* (holotype, P!).

Pogopetalum acutum Benth., London J. Bot. 2: 377. 1843. TYPE: French Guiana. Cayenne, s.d., *J. Martin s.n.* (holotype, K!; isotypes, G!, P not seen).

Shrubs with decumbent branches or trees, 2–15(–30) m. *Leaves* coriaceous, slightly bicolored, green-brown on the abaxial surface and dark green on the adaxial surface; lamina 6.5–18 × 3–8 cm, ovate to oblong, sometimes elliptic, apex long acuminate to acute, base rounded to slightly obtuse, puberulent on the abaxial surface, glabrous on the adaxial surface; secondary veins 6 to 9 pairs, conspicuous; petiole 1–2 cm. *Inflorescences* axillary, 1- to 5-floriferous branches, up to 4 cm; peduncle short, no longer than 1 cm, *Flowers* pentamerous; pedicels to 3 mm; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with the petals white, 4.5–6 × 1.2–1.5 mm, narrowly oblong, densely pilosulose, forming

a beard on the adaxial surface, glabrous on the base; *stamens* 4.5–6 mm, filaments 3.5–4 mm, slightly swelled; anthers ca. 1 mm, basifixed, connective ovate; *pistils* 3.5–4.5 mm, ovary hirsute; style 2.5–3.5 mm, terminal. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum fagifolium* occurs in Guyana (Barima-Waini, Cuyuni-Mazaruni, Demerara-Mahaica, East Berbice-Corentyne, East Demerara, Essequibo Islands-West Demerara, Mahaica-Berbice, Upper Demerara-Berbice, and West Demerara), Suriname (Nickerie), French Guiana (Cayenne), and Brazil (Acre, Amapá, Amazonas, Maranhão, Pará, and Pernambuco). It grows in shrublands, riparian forests, and savanna with trees in sandy soil, between 100 and 300 m elevation.

Phenology. *Emmotum fagifolium* flowers year round and fruits from December to March.

IUCN Red List category. There are many collections of this species occurring over a large area, including areas that are protected and that are not densely populated. It is therefore listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Vernacular names and uses. Bois de'Agouti, harriromanabading, muirachimbé, muira-ximbé, pao de ramo (Howard, 1942b). De Roon (1994) included the following names: candlewood, manobodin, harrariro-manobodin (Guyana), and bois d'agouti (French Guyana). Corrêa (1984) mentioned that the wood is excellent for fire. Its local names in Brazil are muirachimbé and marachaimbé.

Discussion. In the phylogenetic analysis, *Emmotum fagifolium* is resolved as sister species to a clade including *E. glabrum*, *E. celiae*, and *E. yapacanum*. From a phenetic standpoint, however, it is also similar to *E. affine* and *E. conjunctum*. It has ovate to oblong, sometimes elliptic leaves (vs. elliptic to ovate in *E. affine* and oblong to narrowly oblong in *E. conjunctum*) that are puberulent on the abaxial surface (vs. sericeous). The sister clade (*E. glabrum*, *E. celiae*, and *E. yapacanum*) features smaller leaves with fewer, less conspicuous secondary veins, and shorter petioles.

Additional specimens examined. BRAZIL. **Acre:** estr. Isac, aprox. 4 km da cidade, *C. A. Cid Ferreira et al.* 10942 (A). **Amapá:** BR 156, betw. Calçoene & Rio Amapá Grande, 30 km S of Calçoene, *S. Mori & R. Cardoso* 17360 (A, NY). **Amazonas:** Rio Jarí, Monte Dourado, Planalto A, *N. T. Silva* 1006 (A, NY [2]). **Pará:** Belem, Catú, *A. Ducke* 1616 (A, F, MG, NY, R); Turiaçu, Km 6 de BR 106, Maracaçuma–Sta. Elens, *N. A. Rosa & H. Vilar* 2794 (F,

GH, NY); margem da estr. Gurupá, Rio Tajapuri, Km 4, *N. T. Silva & C. Rosario* 5092 (F, GH, NY); alto de Alegria, *E. H. Snethlage* 341 (F). **Pernambuco:** Madeiros Costa Cabo, area proj. Suape, *A. Lima* 22267 (F). FRENCH GUIANA. **Cayenne:** Isle de Cayenne, *J. J. Granville* 9122 (NY, US); Cayenne, *Martin s.n.* (F [photo], GH, K, US [photo]); near rd. (Hwy. D5) from Tonate to Montsinery & Tonnegrade, *L. Skog et al.* 7028 (B, F, G, K, M, NY, US). GUYANA. **Barina-Waini:** Barima River, *J. S. de la Cruz* 3375 (GH, NY). **Cuyuni-Mazaruni:** Kuroba, E on Mazaruni River, 3 km N of confluence of Kamarang River with Mazaruni River, *D. Clarke* 806 (MO, US); Arabapo, Mt. Roraima, *Forest Department* 2829 (K); Pakaraima Mtns., Kako Ameridian village, Kako River, *P. J. M. Maas & L. Y. Th. Westra* 4364 (K); Mazaruni Station, *N. Y. Sandwith* 1547 (B, M, NY). **Demerara-Mahaica:** Soesdyke-Linden Hwy., 2–3 km SW of Timehri airport at jct. of minor rd., *L. J. Gillespie* 2653 (MA, NY); Imbaimadai, Partang River crossing, 1 km from mouth, *L. J. Gillespie & D. R. Smart* 2679 (CTES, NY); Demerara River, *Jenman* 4868 (K); Linden-Soesdyke Hwy., betw. Dora & Maibia Creek, *J. J. Pipoly et al.* 9714 (NY); Yarrowkabra settlement & Forestry Station E & W of Timehri-Linden Hwy., *J. J. Pipoly & H. Godfrey* 7462 (F, NY, US). **East Berbice-Corentyne:** lt. (S) bank upper Canje River W of Digitima Creek, *J. J. Pipoly et al.* 9441 (NY). **Essequibo Islands-West Demerara:** near Bartica, green heart Wallaba forest, *T. A. W. Davis* 1009 (K); Mabura region, Centra, CD 920 rd., *R. C. Ek* 743 (NY); Mabura Hill, 180 km SSE of Georgetown, Mabura main rd., *H. ter Steege & P. del Jager* 400 (B, M, US); W border of Atkinson Field, *H. S. Irwin* 199 (US). **Mahaica-Berbice:** 4 km from Santa Misión, *A. R. A. Gorts-van Rijn* 401 (K). **Upper Demerara-Berbice:** Mackenzie Mines area, vic. E of Utuni, 35 mi. S of Mackenzie, *R. S. Cowan* 39241 (A, NY); 10 km S of Soesdyke on rd. to Linden, behind forest station & along creek, *W. Hahn & S. Tiwari* 4789 (CTES, NY); Atkinson Field Army Barracks, E Bank Demerara, *S. A. Harris* 49 (K); from trail near Camp 18 on R. B. Kurudimi, River Demerara, *L. S. Honenkerk* 131a (K); Sand Hill, 35 mi. up Demerara River, *B. R. Wood* 893 (K). SURINAME. **Nickerie:** area of Kabalebo Dam Project, *N. M. Heyde & J. C. Lindeman* 240 (K).

- 6. *Emmotum floribundum*** R. A. Howard, J. Arnold Arbor. 23(4): 487, tab. 2. 1942. TYPE: Peru. Loreto: Mishuyacu, near Iquitos, 100 m, forest, Apr. 1930, *A. Klug* 1212 (holotype, F!; isotype, US!).

Shrubs or tree, to 10 m. *Leaves* coriaceous, sharply bicolored, green-brown on the abaxial surface and dark green and shiny on the adaxial surface; lamina 8–14 × 4–8 cm, ovate, elliptic, or oblong, sericeous on the abaxial surface, glabrous on the adaxial surface, apex acute or mucronate, base rounded to slightly obtuse; secondary veins 8 to 11 pairs, conspicuous; petiole 1.5–2.5 cm. *Inflorescences* axillary, sometimes cauliflorous, 1- to 3-floriferous branches, up to 4 cm; peduncle short, no longer than 1 cm. *Flowers* pentamerous; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with petals

white, 5.5–6 × 1.2–1.5 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 5.5–6 mm, filaments 4.5–5 mm, slightly swelled; anthers ca. 1.2 mm, dorsifixed, connective ovate; *pistils* 5–5.5 mm, ovary hirsute; style 3.5–4 mm, centric. *Fruit* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum floribundum* occurs in Colombia (Amazonas, Caquetá, and Vaupés), Venezuela (Amazonas), Guyana, Peru (Loreto), and Brazil (Acre and Amazonas). It grows in riparian forest that is susceptible to flooding and in shrubland between 80 and 150 m elevation.

Phenology. *Emmotum floribundum* flowers from November to August and fruits from October to July.

IUCN Red List category. The few known collections of this species are scattered over a large area, including areas that are protected and that are not densely populated. It is therefore listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Vernacular names and uses. In Peru it is known as ingaina (Howard, 1942b) and in Venezuela as yurí de caracol.

Discussion. According to our analysis, *Emmotum floribundum* is the sister species of *E. acuminatum*. Both species have dorsifixed anthers and a glabrous ovary with a long eccentric style. It differs from *E. acuminatum* in its ovate, elliptic, or oblong lamina (vs. oblong to ovate, rarely elliptic) that is sericeous on the abaxial surface (vs. puberulent) and with eight to 11 pairs of secondary veins (vs. six to nine pairs).

Additional specimens examined. BRAZIL. **Acre:** Mâncio Lima, Ramal do Banho, 5 km NW of Mâncio Lima, *D. C. Daly et al.* 9050 (NY). COLOMBIA. **Caquetá:** Región Araracuara, *D. Restrepo & A. Matapi* 443 (F, MO). **Vaupés:** Río Apaporís, Raudal Yayacopi (la playa) & vic., *R. E. Schultes & I. Cabrera* 15504 (NY). GUYANA. **Cuyuni-Mazaruni:** mouth of Kako River (upper Mazaruni tributary), *A. S. Pinkus* 193 (MO). PERU. **Loreto:** Quebrada Shushuma near rd. to Mapa Cocha, ca. 17 km from Iquitos, *S. MacDaniel & M. Y. Rimachi* 22469 (F); carr. Zungaro Cocha, cerca de quebrada Shushuma, *M. Y. Rimachi* 6531 (F, NY, US). VENEZUELA. **Amazonas:** Río Sipapo, 4–5 km arriba de la boca del Río Guyapo, ca. la población piaroa de San Felipe (Raudalito), *G. Carnevali et al.* 1700 (MO); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro & Brazo Casiquiare, *H. L. Clark & P. Maquirino* 8078 (MO, NY); San Carlos de Río Negro, 20 km de la confluencia del Río Negro y Brazo Casiquiare, *F. Delascio et al.* 9625 (VEN); Río Baría, *A. Gentry & B. Stein* 47359 (A, MO, NY, VEN); Caño Caname, afluente derecho (oriental) del medio Río Atabapo, sabana de Cucurital, 20 km E de la boca, *O. Huber et al.* 3730 (A, NY, VEN);

sabana ubicada a unos 10 km S del Río Autana y unos 15 km al SW del Cerro Autana, *O. Huber et al.* 4053 (A, NY [2]); Sabana Morocoto just W of Cerro Morocoto, below San Fernando de Atabapo, *J. S. L. Level* 16 (A, NY, VEN); N de Raudalito, Río Sipapo, *G. Romero & F. Guánchez* 1627 (GH, NY, VEN); Santa Rosa de Ucata, *G. Romero & F. Guánchez* 1862 (GH, MO, NY); base del Cerro de la Neblina, Río Baría, from the Río Mawarinuma, *W. W. Thomas et al.* 3464 (F, MO, NY, VEN); in Sabanita Morocoto (rt. bank 2 km below mouth of Atabapo), *J. J. Wurdack & L. S. Adderley* 42696 (GH, NY, VEN).

7. *Emmotum fulvum* R. A. Howard, J. Arnold Arbor. 23(4): 493, tab. 4. 1942. TYPE: Venezuela. Bolívar [Amazonas]: Arabupu, vic. of Mt. Roraima, 4200 ft., 21 Dec. 1938, *Pinkus* 87 (holotype, NY!; isotypes, BR not seen, F!, U not seen, US!).

Shrubs or tree, to 30 m. *Leaves* coriaceous, sharply bicolored, brown ferruginous to golden on the abaxial surface, dark green and shiny on the adaxial surface; lamina 10–16 × 4–6 cm, ovate to narrowly ovate, velvety on the abaxial surface, glabrous on the adaxial surface, apex narrowly acute, base rounded or slightly obtuse; secondary veins 6 to 9 pairs; petiole ca. 1.5 cm. *Inflorescences* axillary, sometimes cauliflorous, 1- to 3-floriferous branches, up to 2 cm; peduncle short, no longer than 1.5 cm. *Flower* pentamerous; pedicels up to 3 mm; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with petals white, 5.5–6 × 1–1.2 mm, narrowly oblong, densely pilosulose, forming a barbed indument on the adaxial surface; *stamens* 5–5.5 mm, filaments 4.5–5 mm, slightly swelled; anthers 1–1.2 mm, basifixed, connective ovate; *pistils* 5–5.5 mm, ovary hirsute; style 3–3.5 mm, centric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum fulvum* is endemic to Venezuela, where it has been collected in the state of Bolívar. It is possibly found in Guyana (de Roon, 1994). It grows in low, medium to tall forests on tepui slopes, between 850 and 1700 m elevation.

Phenology. *Emmotum fulvum* flowers from November to May.

IUCN Red List category. The few known collections of this species are scattered over a large area, including several areas that are protected and that are not densely populated. It is therefore listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Vernacular names and uses. In Venezuela it is known as apory-ban-yek (Pemón).

Discussion. According to the phylogenetic analysis, *Emmotum fulvum* is the sister species of *E. conjunctum*, but the former has a narrowly ovate lamina with a dense velvety indument on the abaxial surface with long hairs (vs. oblong to narrowly oblong and sericeous on the abaxial surface).

Additional specimens examined. VENEZUELA. **Bolívar:** vic. of Arapubu [Arobopo], *A. P. Pinkus* 87 (GH, NY [2]); Cerro Uei, entre Luepa y Cerro Venamo, *J. A. Steyermark & Nilsson* 466 (A, NY, VEN); Macizo de Chimantá, Amurí-tepui, *J. A. Steyermark & J. J. Wurdack* 1367 (A, VEN); Ptari-tepui, *J. A. Steyermark* 60671 (A, NY, VEN); Macizo de Chimantá, *J. A. Steyermark* 75141 (NY, VEN); SW face of Chimanta-tepui (Torono-tepui), above Río Tirica, *J. A. Steyermark* 75430 (G, NY [2]); Cerro Venamo, *J. A. Steyermark et al.* 92715 (A, F, NY, VEN).

8. *Emmotum glabrum* Benth. ex Miers, Ann. Mag. Nat. Hist., ser. 3, 4: 366. 1859. TYPE: Venezuela. Amazonas: Rio Guainia & Rio Casiquiare in Brasilia Septentrionali, *R. Spruce* 3536 (lectotype, designated by de Roon [1994: 98], K! [specimen on blue card]; isotypes, G!, K!, MO!, NY!, P not seen). Figure 4.

Emmotum argenteum Gleason, Bull. Torrey Bot. Club 58: 386. 1931. TYPE: Venezuela. Amazonas: Mt. Duida, on slopes at Central camp, 4800 ft., [*G. H. H. Tate*] 564 (holotype, NY!).

Emmotum ptarianum Steyermark, Fieldiana, Bot. 28(2): 341. 1952. TYPE: Venezuela. Bolívar: collected in vic. of “Misia Kathy Camp,” SE-facing slopes, Ptari-tepui, 1585–1600 m, 10–11 Nov. 1944, *J. A. Steyermark* 59974 (holotype, F!; isotypes, MO not seen, NY!, P not seen, US!, VEN!).

Shrubs to trees, to 20 m. *Leaves* subcoriaceous, nonbicolored, dark green or brown on both surfaces; lamina 5–13 × 3–6 cm, elliptic to oblong, sometimes ovate, puberulent on the abaxial surface, with few, long, white, and adpressed hairs, especially along the main nerve, glabrous on the adaxial surface, apex long acuminate, up to 2 cm, sometimes acute, base slightly obtuse or slightly attenuate; secondary veins 2 to 5 pairs, inconspicuous; petiole 0.5–0.8(–1) cm. *Inflorescences* axillary, sometimes cauliflorous, 1-floriferous branches, up to 2 cm, peduncle short, no longer than 1.5 cm. *Flowers* pentamerous; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with petals white, 3.5–4 × ca. 1 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 3–4 mm, filaments 2.8–3 mm, slightly swelled; anthers 1–1.2 mm, basifixed, connective ovate; *pistil* 4–4.5 mm, ovary hirsute; style 2.5–3 mm, centric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

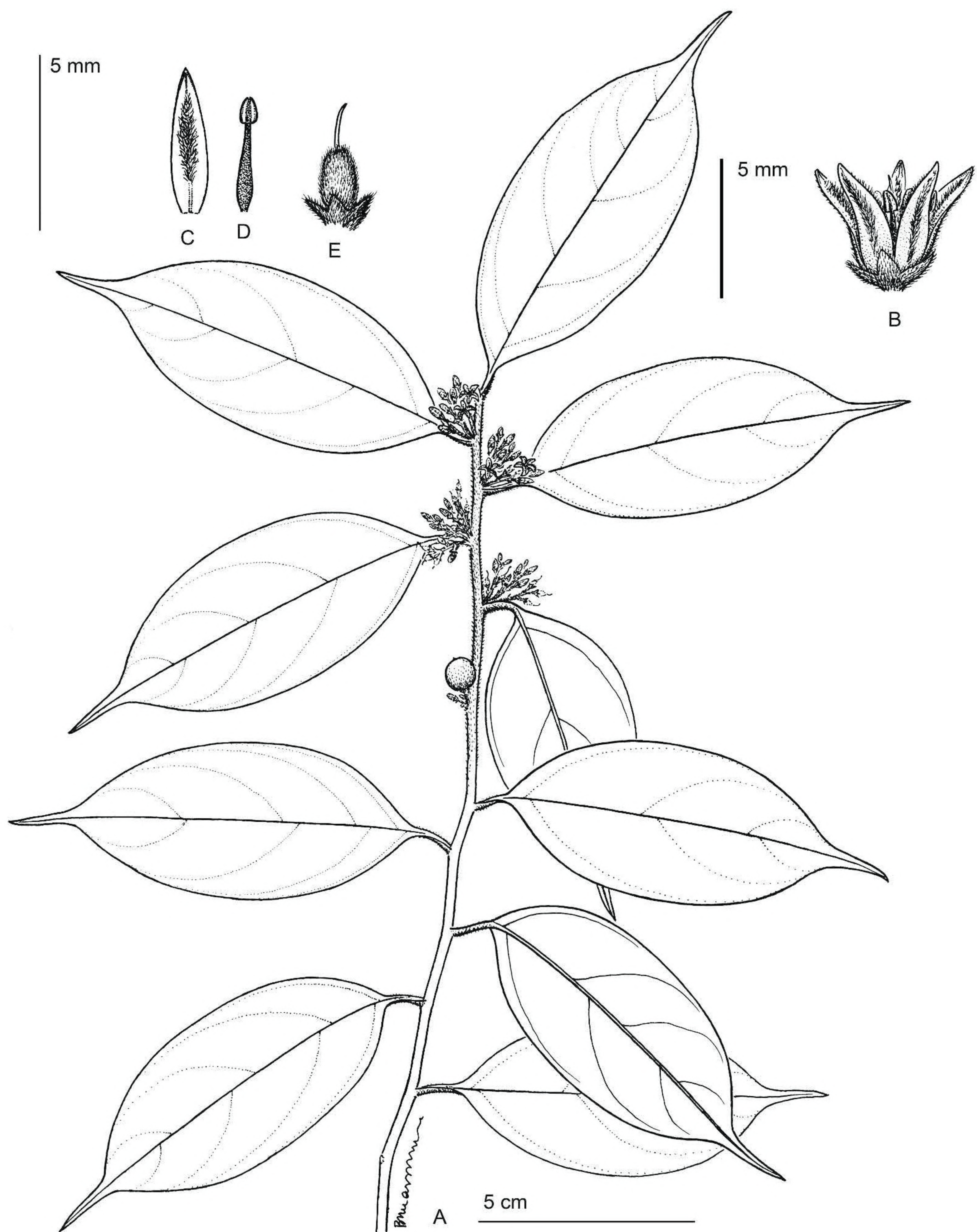


Figure 4. *Emmotum glabrum* Benth. ex Miers. —A. Habit. —B. Flower. —C. Petal inner surface. —D. Stamen. —E. Flower with petals removed and pistil visible. Drawn from J. A. Steyermark & B. K. Holst 130635 (VEN).

Distribution and ecology. *Emmotum glabrum* occurs in Colombia (Vaupés), Venezuela (Amazonas and Bolívar), Guyana (Potaro-Siparuni and Cuyuni-Mazaruni), Peru (San Martín), and Brazil (Amazonas). The collection from Peru represents a clear disjunction in the distribution of this species; the collection from Brazil is very near the Venezuelan frontier. It

grows in riparian forest, montane forests, shrubland, tepui meadows, and open rocks on sandstones, between 100 and 1800 m elevation.

Phenology. *Emmotum glabrum* flowers and fruits from October to May.

IUCN Red List category. There are many known collections of this species scattered over a large area, including protected areas and areas that are not densely populated, and it is therefore listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Discussion. In the phylogenetic analysis, *Emmotum glabrum* is the sister species of a clade including two species, *E. celiae* and *E. yapacanum*. *Emmotum glabrum* differs from *E. celiae* by the larger lamina (5–13 cm vs. 2–5 cm), the acuminate apex (vs. acute to slightly mucronate), and the number of secondary veins (two to five vs. two to three pairs); it differs from *E. yapacanum* by its shorter peduncle (less than 1.5 cm vs. 4 cm).

Emmotum glabrum has been registered three times in Brazil (Engler, 1872; Carvalho et al., 1973; Prance & Johnson, 1992), but the collections mentioned in the first two publications belong to *E. nitens* and *E. amazonicum*, respectively. Only the collections from Serra do Aracá, very near the Venezuelan border, belong to *E. glabrum* (Prance & Johnson, 1992).

Emmotum glabrum was originally described by George Benthham in 1859 from the collection *Richard Spruce 3536* from Amazon State (Venezuela) as type. Two sheets from the personal herbarium of Benthham were deposited at Kew and neither was annotated by him as type material. These two specimens were studied by A. C. de Roon in 1993 and labeled as holotype (collection with the flowers mounted on the blue card) and isotype, respectively. One year later, he published the treatment of the family for the *Flora of the Guianas* (de Roon, 1994), citing *R. Spruce 3536* as the holotype. In doing so, he de facto lectotypified the name with that specimen.

Additional specimens examined. BRAZIL. **Amazonas:** Serra da Aracá, parte SE da Serra Norte, *Amaral do. I. L. 1603* (MO, NY); Margenes do R. da Serra Aracá, *M. A. Rosa & S. B. Lira 2313* (A, NY); Serra da Aracá, parte SE da Serra Norte, *A. S. Tavares & M. G. Silva 51* (NY); Serra da Aracá, parte SE da Serra Norte, *A. S. Tavares & M. G. Silva 82* (NY). COLOMBIA. **Guainía:** Maimachi, Serranía del naquén, Cerro Minas, alrededores del Helipuerto 15 y camino hasta la cima del cerro, *C. Barbosa & S. Madriñan 8362* (MO). GUYANA. **Cuyuni-Mazaruni:** Mazaruni-Potaro Region, Upper Mazaruni River Basin, Pakaraima Mtns. Peak, N of Karowrieng Rivers, *J. J. Pipoly & K. Alfred 7717* (B, F, GH, M, MO, NY, US); Upper Mazaruni River Basin, SE ridge of Merume Mtns., *S. S. Tillett et al. 44832* (A, F, K, NY). **Potaro-Siparuni:** Kaieteur savannah, Potaro Rivers, *G. S. Jenman 1050* (K); Kaieteur plateau, *B. J. Maguire & B. Fanshane 23339* (A, F, K, MO, NY, VEN). PERU. **San Martín:** Chazuta, Río Huallaga, *G. Klug 3990* (F, GH, K, NY, US). VENEZUELA. **Amazonas:** Región Duida Marahuaca, *V. Barnes 35* (VEN); Cerro Aracamuni,

G. Carnevali et al. 2583 (VEN); laderas SE del Cerro Huachamacari, *F. Delascio 12356* (VEN); slope of Cerro de Marahuaca, *R. L. Liesner 17738* (MO, NY); on plateau of Duida above Culebra, *R. L. Liesner 18182* (MO, NY); slope of Huachamacari, *R. L. Liesner 18342* (MO, NY, VEN); Cerro Aracamuni, *R. L. Liesner & G. Carnevali 22670* (A, MO, NY); Cerro Marahuaca, Sima area, *R. L. Liesner 25057* (A, NY); Cerro Sipapo (Paráque), below escarpment at camp, *B. J. Maguire & L. Politi 27562* (GH, NY); Cerro Duida, *B. J. Maguire & B. Maguire, Jr. 29165* (GH, NY, VEN); Río Guainía, just S of Maroa, *B. J. Maguire 36447* (A [2], COL, NY [2]); Cerro de la Neblina, on Cañón Grande slopes E of Cumbre Camp, *B. J. Maguire et al. 42177* (A, NY); Cerro de la Neblina, Río Yatua, Cañón Grande, *B. J. Maguire et al. 42230* (A, NY, VEN); Guainía entre el Río Negro y el Casiquiare, *R. Spruce 3536* (BM, F, G, GH, K, MO [photo], NY, US [photo]); faldas del extremo N del Cerro Duida, al SO de la comunidad de Culebra, *J. A. Steyermark et al. 126138* (A, NY, VEN); Pimichín, Guainía, *L. L. William 14946* (A, VEN). **Bolívar:** base central del Guaquinima-tepui, quebrada Martínez, *G. Aymard C. 5985* (MO, VEN); Cerro Guaquinima, camp 4, *B. Boom 9370* (A); Amaruay-tepuy, *B. K. Holst & R. L. Liesner 2828* (A, MO, VEN); Piar, Río Acanan, Guaruma, 5 km SW by air of confluence with Río Carrao, E of Auyan-tepui, *B. K. Holst & R. L. Liesner 2855* (A, MO, NY); Uaiparú, 50 km al NNW de Icabarú, *O. Huber & A. Fernández 11328* (NY, VEN); Cerro Venamo, a lo largo del afluente derecho (O) subiendo el Río Venamo, descendiendo el río desde el campamento, *J. A. Steyermark et al. 92366* (A, NY, VEN); Cerro Marutaní, NNW of camp 2 along tributary of Río Carla, *J. A. Steyermark et al. 124070* (MO, NY, VEN); Cerro Marahuaca, *J. A. Steyermark & B. Holst 130635* (A, MO); Chimantá, vic. camp 3, beside small stream, lower slopes of Tirepón-tepui, *J. J. Wurdack 34043* (A, NY, VEN); middle slopes of Sarvén tepuí, *J. J. Wurdack 34100* (A, NY).

9. *Emmotum yapacanum* R. A. Howard, Mem. New York Bot. Gard. 29: 66, fig. 56. 1978. TYPE: Venezuela. Amazonas: Cerro Yapacana, *B. Maguire, R. S. Cowan & J. J. Maguire 30518* (holotype, NY!; isotype, A!). Figure 5.

Shrub or trees, to 3 m. *Leaves* subcoriaceous, nonbicolored, dark brown on both surfaces; lamina 6–7 × 2.8–3.2 cm, elliptic, pubescent on the abaxial surface, glabrescent, apex long acuminate, to 2.5 cm, sometimes acute; secondary veins 2 to 3 pairs, inconspicuous; petioles 0.5–0.8 cm. *Inflorescences* axillary, sometimes cauliflorous, 1-floriferous branches, to 4 cm; peduncle ca. 4 cm. *Flowers* pentamerous; *calyx* campanulate, sepal lobes ca. 1 × 0.7 mm, triangular; *corolla* with petals 4.5–5 × ca. 1 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 3.5–4 mm, filament 2.5–4 mm, slightly swelled; anthers 1–1.2 mm, basifixed, connective ovate; *pistils* 4–4.5 mm, ovary hirsute; style 2.5–3 mm, centric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

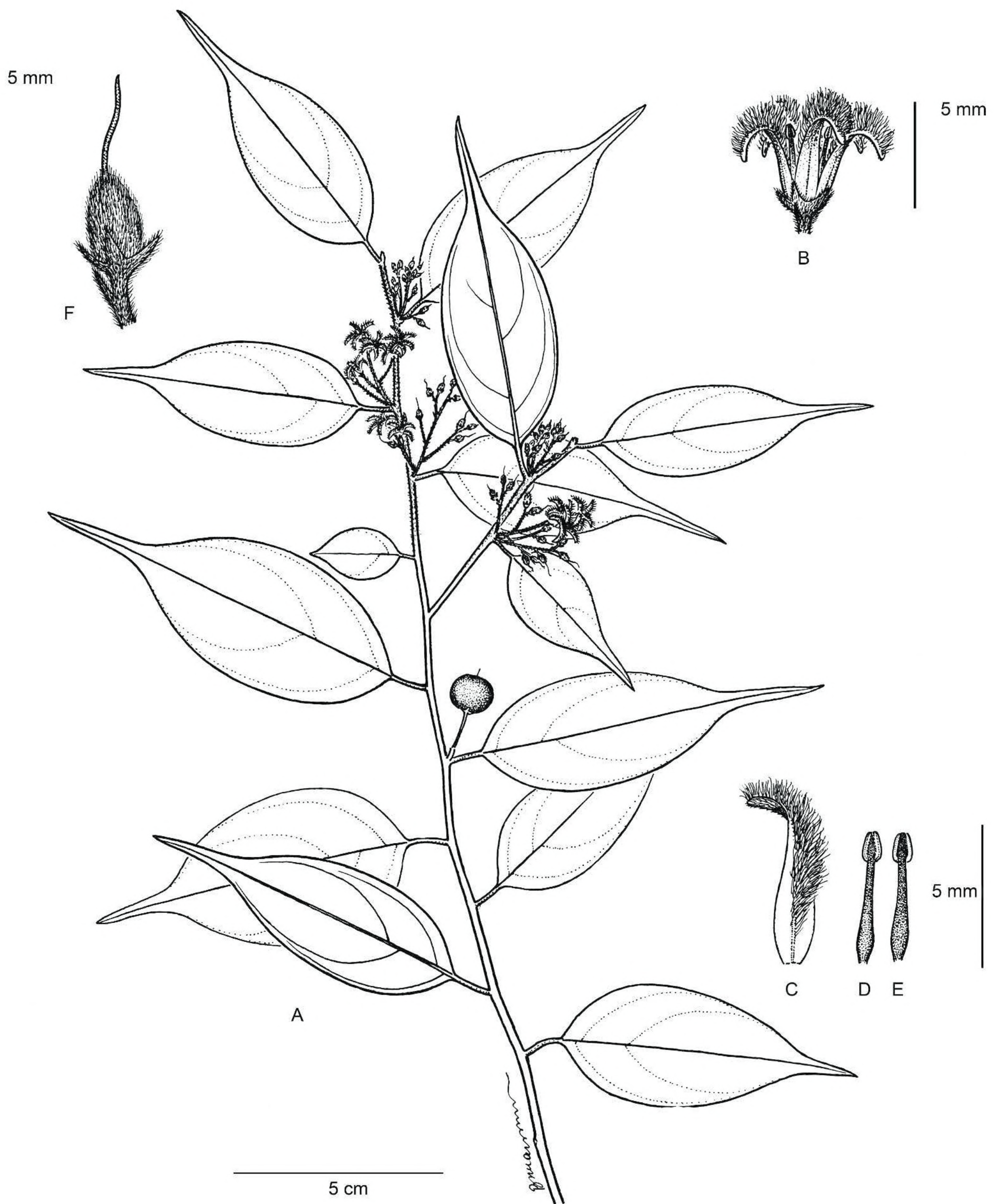


Figure 5. *Emmotum yapacanum* R. A. Howard. —A. Habit. —B. Flower. —C. Petal inner surface. —D, E. Stamens. —F. Flower with petals removed and pistil visible. Drawn from J. A. Steyermark & G. Bunting 103139 (VEN).

Distribution and ecology. *Emmotum yapacanum* is endemic to Venezuela. It has only been collected in Amazonas State. It grows on shrublands on sandstone-derived substrates between 800 and 1300 m elevation.

Phenology. *Emmotum yapacanum* flowers between January and March.

IUCN Red List category. *Emmotum yapacanum* is only known from three collections. It could be best listed as Data Deficient (DD). However, because it is restricted to isolated sandstone table mountain slopes and summits in a completely inaccessible area, it could alternatively be listed at Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Discussion. *Emmotum yapacanam* is the sister species of *E. celiae* in the phylogenetic analysis. From a phenetic point of view it is very similar to *E. glabrum*, from which it differs by its longer peduncle (ca. 3 cm vs. ca. 1.5 cm long). It is possible that *E. yapacanam* represents an extreme variation of *E. glabrum* with a long peduncle. However, more material from the type locality in the Cerro Yapacana is necessary.

Additional specimens examined. VENEZUELA. **Amazonas:** NW slopes of Yapacana, *B. Maguire et al.* 30518 (NY); cumbre del Cerro Yapacana, *J. S. Steyermark & G. Bunting* 103139 (A, MO, NY, VEN).

Ib. *Emmotum* sect. *Brevistyla* Engl., Fl. Bras. (Martius) 12(2): 44. 1872. TYPE: *Emmotum nitens* (Benth.) Miers [= *Pogopetalum nitens* Benth.], s.d., *C. A. Gardner* 3309 (lectotype, designated by Duno et al. [2007: 308], K!).

Pogopetalum Benth., Proc. Linn. Soc. London 1(10): 87–88. [6 Apr.] 1841. TYPE: *Pogopetalum orbiculatum* Benth. [= *Emmotum orbiculatum* (Benth.) Miers] (lectotype, designated here).

This section is characterized by flowers with the petals lanate within, but with only two clusters at the base and the apex, rarely these trichomes are laxly continuous along the inner surface of the petal; filaments that are dilated both at the base and the apex; anthers that are oblong, with the connective elliptic in shape and prolonged at the apex; the ovary distinguished by the short style, less than 0.5 mm long; and by the absence of eccentric styles. This section includes *Emmotum amazonicum*, *E. harleyi*, *E. nitens*, and *E. orbiculatum*.

1. *Emmotum amazonicum* Duno & Carnevali, sp. nov. TYPE: Brazil. Amazonas: Manaus, Rio Tarumá, silva inundabilis, 27 Oct. 1943 (fl.), *A. Ducke* 1413 (holotype, NY!; isotypes, GM not seen, IAN not seen, US!).

Species *Emmoto nitenti* (Benth.) Miers affinis, sed ab eo foliis concoloribus abaxialiter puberulis (vs. dense pubescentibus), nervis secundariis 11 ad 14 et ovario glabro differt.

Shrubs or tree, up to 12 m high. **Branches** cylindrical, sulcate, covered by fine tomentum. **Leaves** exstipulate, coriaceous, sulcate, puberulent, not bicolored, dark brown on both surfaces; lamina 7–10 × 3–5 cm, elliptic to elliptic-oblong, adaxial surface glabrous, abaxial surface brown-yellow puberulent, apex acute, base rounded, margin entire, slightly revolute; secondary veins 11 to 14 pairs, 3–5

mm between them; petiole 1–1.5 cm. **Inflorescence** axillary, a short panicle, flower pentamerous, hermaphroditic; bract triangular, ca. 1 × 1 mm, adaxial surface glabrous, abaxial surface sericeous-tomentose; pedicel articulate; **calyx** campanulate, sepal lobes ca. 0.5 × 0.5 mm, triangular, concave, with the apex acute, adaxial surface glabrous, abaxial surface tomentose; **corolla** with petals reflexed when mature, ca. 2.6 × 1 mm, adaxial surface sericeous-tomentose, abaxial surface with 2 tufts of hair at the base and apex; apex acute, with a diminute end on the adaxial surface; **stamens** incurved, filaments ca. 2 mm, slightly thickened with a dilated apex, connective elliptic, apex slightly prolonged; anthers basifixed, cordate, ca. 1.5 mm; **pistils** with the ovary globose, glabrous, style short and curved at the apex, ca. 0.5 mm long, stigma obsolete, diminute 3-lobate. **Fruit** a drupe, subglobose, ca. 1.5 × 2.4–2.5 cm (diam.), unilocular, sometimes with the crest not very well developed; seed solitary.

Distribution and ecology. *Emmotum amazonicum* is endemic to Brazil, where it is only known from the states of Amazonas; there it grows in forest between 0 and 100 m elevation.

Phenology. *Emmotum amazonicum* has been collected in flower in October and fruit in January.

IUCN Red List category. Because this species is only known from three collections, it is listed as Data Deficient (DD) according to IUCN Red List criteria (IUCN, 2001).

Discussion. In the current phylogenetic analysis, *Emmotum amazonicum* is the sister species of a clade that includes three taxa: *E. harleyi*, *E. nitens*, and *E. orbiculatum*. From a strictly phenetic point of view, however, it is most similar to *E. nitens*. *Emmotum amazonicum* differs from *E. nitens* in the lamina that is not strongly bicolored and with a dense indument on the abaxial surface, the number of secondary veins (11 to 14 vs. six to eight pairs), and the glabrous ovary. Furthermore, this taxon is known to occur only in the Brazilian Amazon Basin (Amazonas), to the north of the distribution of *E. nitens*, which occurs in the southern part of Amazonas, and from Bahia, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, and Pernambuco, as well as Bolivia (Beni, La Paz, and Santa Cruz).

Paratypes. BRAZIL. **Amazonas:** 20 km NW of Manaus, *B. W. Nelson & S. P. Nelson* 1045 (NY); Reserva Florestal Ducke, Manaus–Itacoatiara, Km 26, *J. M. Brito & P. A. C. L. Assunção* 40 (K, MO); Reserva Florestal Ducke, Manaus–Itacoatiara, Km 26, *A. Vicentini* 828 (K, MO, NY).

- 2. *Emmotum harleyi*** Duno, Novon 17(3): 306–308, fig. 1. 2007. TYPE: Brazil. Bahia: 19.5 km SE of Morro do Chapéu on BA052, rd. to Mundo Novo, by Rio Ferro Doido, ca. 900 m, ca. 11°38'S, 41°02'W, 2 Mar. 1977 (fl.), *R. M. Harley, S. J. Mayo, R. M. Storr, T. S. Santos & R. S. Pinheiro* 19248 (holotype, K!; isotypes, K!, NY!). Figure 6.

Shrubs to small trees, to 5 m. *Leaves* coriaceous, sharply bicolored, dark green and shiny adaxially, yellow or golden abaxially; lamina 5–10 × 3–4.5 cm, elliptic or widely elliptic, rarely ovate or narrowly ovate, apex acute, rarely acuminate, attenuate, shortly acuminate, or emarginate, base rounded, margin entire, slightly revolute; secondary veins 9 to 11 pairs, well developed but hidden by a dense indument; adaxially glabrous, abaxially densely tomentose with crisped hairs ca. 0.2 mm long; petioles 1.3–1.5 cm. *Inflorescences* axillary, 1- to 4-floriferous branches per axil. *Flowers* pentamerous; *calyx* campanulate, sepal lobes, ca. 1 × 0.8 mm, triangular; *corolla* with white petals, 2.5–3 × ca. 1 mm, ovate or narrowly ovate, slightly bearded on the inner surface; *stamens* 2.5–3 mm, filament 1.5–1.8 mm, basally dilated; anthers basifixed, connective elliptic, slightly prolonged at the apex; *pistils* with the ovary glabrous; style terminal, very short, no longer than 0.5 mm. *Fruit* 1–1.2 × 1–1.5 cm (diam.).

Distribution and ecology. *Emmotum harleyi* is endemic to Brazil, where it is only known from the Chapada Diamantina including the Serra do Tombador in Bahia. It grows mainly in campo rupestre over white crystalline sand rock, between 800 and 1200(1450) m elevation, and more rarely on mata ciliar at 500 m.

Phenology. *Emmotum harleyi* flowers from September to July and fruits from September to June.

IUCN Red List category. The information about the population status of this species is far from complete to produce a precise conservation evaluation, but some general information can be gathered from specimen labels. *Emmotum harleyi* occurs along discontinuous patches in an area of ca. 100,000 km². There are numerous botanical collections, including some made inside protected areas such as Parque Municipal de Mucugê, Parque Municipal Natural da Serra das Almas, Parque Nacional da Chapada Diamantina, and Santuario Ecologico do Largo do Queiroz, among others. Despite the fact that the cerrado and campo rupestre are two of the most threatened ecosystems in northeastern Brazil, the

populations of this species seem to be large enough to be excluded from any category of protection according to IUCN Red List criteria (IUCN, 2001) or listed as Least Concern (LC).

Vernacular name. Aderno.

Discussion. In the phylogenetic reconstruction, *Emmotum harleyi* is the sister species of a clade with two species, *E. orbiculatum* and *E. nitens*. However, from a phenetic point of view it is more similar to *E. nitens* because in both species the filament is basally dilated, the anthers are basifixed with the connective elliptic and slightly prolonged at the apex, and the pistil has a short style, less than 0.5 mm long. However, *E. harleyi* has long, erect, and crisped hairs on the abaxial surface of the leaves (vs. short, appressed, straight hairs in *E. nitens*), the inner surface of the petals has a continuous band of hairs along the midvein (vs. two tufts of hair at the base and the apex), and a glabrous ovary (vs. hirsute). Furthermore, *E. harleyi* occupies a different habitat (campo rupestre vegetation over white crystalline sand rock, between [500–]800 and 1450 m) and a different geographical area of distribution (Bahia). *Emmotum nitens* is found between 300 and 1000 m in cerrado vegetation on clay soils in the states of Bahia, Distrito Federal, Goiás, Minas Gerais, and Pernambuco in Brazil and the departments of Beni, La Paz, and Santa Cruz in Bolivia. *Emmotum orbiculatum* (Benth.) Miers occurs in the Amazon Basin and is distinguished by its orbicular leaves.

Additional specimens examined. BRAZIL. **Bahia:** área antropizada, *M. L. Guedes et al.* 4750 (K, SPF); 4 km S of Mucugê, on rd. from Cascavel by Rio Cumbuca, *R. M. Harley et al.* 16055 (K, NY); 4 km S of Mucugê, on rd. from Cascavel by Rio Cumbuca, *R. M. Harley et al.* 16056 (K); betw. 2.5 & 5 km S of Vila do Rio de Contas on side rd. to W of the rd. to Livramento, *R. M. Harley et al.* 20136 (NY, US); 2–9 km da cidade na estrada a Arapiranga (furna) para o aeroporto, *R. M. Harley et al.* 26113 (MO, NY); Serra da Chapadinha, entre Chapadinha e Brejões, *E. Melo et al.* 1636 (SPF); arredores de Lençóis, caminho para Barro Branco, *S. A. Mori* 12940 (A, NY); a 6 km ao SW de Mucugê, *S. A. Mori* 13410 (A, NY); Serra das Almas, a 5 km ao NW de Rio de Contas, *S. A. Mori & F. Benton* 13526 (A, NY).

- 3. *Emmotum nitens*** (Benth.) Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 180. 1852. Basionym: *Pogopetalum nitens* Benth., London J. Bot. 2: 377. 1843. TYPE: Brazil. Goiás: s.d., *C. A. Gardner* 3309 (lectotype, designated by Duno et al. [2007: 308], K!; isotypes, G!, K!, NY!).

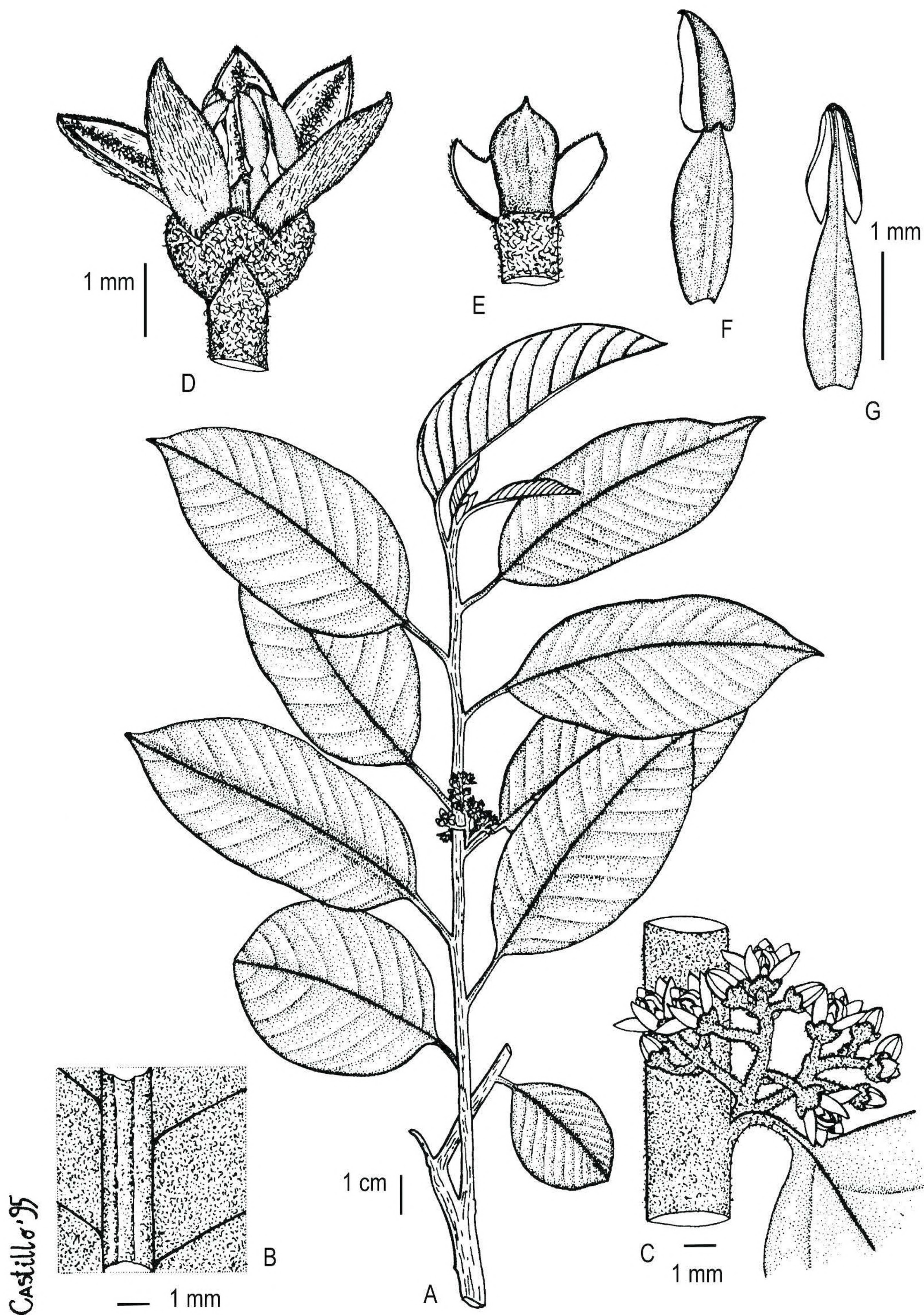


Figure 6. *Emmotum harleyi* Duno. —A. Habit. —B. Detail of the leaf indument (abaxial surface). —C. Detail of the inflorescence. —D. Flower. —E. Detail of the pistil. —F. Stamen, outside surface. —G. Stamen, inner surface. Drawn from the holotype, *R. M. Harley et al.* 19248 (K).

Emmotum faia Kuhlman, Arch. Jard. Bot. Rio de Janeiro 26: 45, estampa 1 (s.n). 1982, nom. nud.
Schnizleinia nitida Mart. ex Engl., Fl. Bras. (Martius) 12(2): 46. 1872, nom. nud., in syn.
Siagonanthus sericeus Pohl ex Engl., Fl. Bras. (Martius) 12(2): 46. 1872, nom. nud., in syn.

Shrubs to trees, to 10 m. *Leaves* coriaceous, sharply bicolorous, light green or grayish on the abaxial surface, dark green and shiny on the adaxial surface; lamina (5–)6–12 × 3–7 cm, oblong, elliptic, or ovate, apex acuminate to acute, rarely mucronate, base rounded, sericeous, rarely tomentose on the abaxial surface, glabrous on the adaxial surface; secondary veins 6 to 8 pairs, conspicuous; petiole 1.5–2.5 cm. *Inflorescences* with 1- to 5-floriferous branches, up to 4 cm; peduncles to 1 cm. *Flowers* pentamerous; pedicels to 3 mm; *calyx* campanulate, sepal lobes ca. 1.5 × 1.5 cm, triangular to widely triangular; *corolla* with the petals white, 3.5–4 × 1–1.2 mm, narrowly oblong, pilosulose on the adaxial surface, on the base, and near the apex, rarely continuous or glabrous; *stamens* 2.5–3 mm, filaments to 2 mm long, basally dilated; anthers basifixed, connective elliptic, slightly prolonged at the apex; *pistils* 1.5–2 mm, ovary hirsute or glabrous; style up to 0.5 mm, eccentric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum nitens* is found in Brazil (Amazonas, Bahia, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, and Pernambuco) and Bolivia (Beni, La Paz, and Santa Cruz). It grows in savannas (cerrado) between 300 and 1000 m elevation.

Phenology. Flowering and fruiting occur year round.

IUCN Red List category. *Emmotum nitens* is a common species in the Brazilian cerrado. It occurs along a continuous area of ca. 2,000,000 km². There are numerous botanical collections, including some made inside protected areas. Despite the fact that the cerrado is one of the most threatened ecosystems in Brazil, the populations of this species seem to be large enough for this species to be excluded from any category of protection according to IUCN Red List criteria (IUCN, 2001), or alternatively could be listed as Least Concern (LC).

Vernacular names and uses. In Brazil it is known as faia (Ferreira & de Abreu, 1982; Corrêa, 1984).

Discussion. In the current phylogenetic analysis, *Emmotum nitens* is the sister species of *E. orbiculatum*. These two species, together with *E.*

amazonicum and *E. harleyi*, form a very distinct clade based on the combination of petals pilose on the abaxial surface with two clusters of hair at the base and the apex or almost glabrous, stamens with the filament dilated at the base, the anthers basifixed with the connective elliptic and slightly prolonged at the apex, and the ovary with a short style, less than 0.5 mm long. *Emmotum orbiculatum* has widely oblongate, widely elliptic, or widely ovate lamina with the apex mucronate. *Emmotum amazonicum* has an elliptic to elliptic-oblong lamina and a glabrous ovary.

The authors of *Emmotum faia* (Ferreira & de Abreu, 1982) did not explicitly typify the name, thus making it invalid under Article 37.1 of the *International Code of Botanical Nomenclature* (McNeill et al., 2006). However, it is obvious from the description and illustration that this entity is referable to *E. nitens*.

Additional specimens examined. BRAZIL. **Amazonas:** Rio Tarumá, cachoeira baixa, A. Ducke 1413 (IAN, MG, NY, US). **Bahia:** Serra ca. 30 km W of Barreiras, W. R. Anderson et al. 36528 (F, MO, US); Espigão Mestre, ca. 100 km WSW of Barreiras, W. R. Anderson et al. 36782 (F, MO, NY); Serra Acurua, Blanchet 2889 (BM, G, GH, NY, US); entre Ajuda e Porto Seguro, A. P. Duarte 6636 (CTES); entre Brejão e Iracema, região de Serra Sincorá, R. L. Fróes 20196 (NY, US); 2–9 km da cidade na estrada a Arapiranga (furna) para o aeroporto, área de inundação da Barragem do São Bartolomeu, Rio Taboca, E. P. Heringer et al. 1383 (MO, R, US); Bacia do Rio São Bartolomeu, E. P. Heringer et al. 1791 (K, MO, NY, US); Córrego, capoeira do Bálsamo, 10 km E of Brasília, H. S. Irwin et al. 8378 (F, GH, MO, NY); vic. Paranóia, H. S. Irwin et al. 11253 (F, GH, MO, NY, US); 10 km NW of Planaltina, H. S. Irwin et al. 13190 (F, GH, MO, NY); Córrego Alogado, Parque Mun. Gama, ca. 20 km SW of Brasília, H. S. Irwin et al. 14098 (F, G, GH, MO, NY, US); rodovia a Livramento do Brumado/Rio de Contas, S. A. Mori et al. 12280 (A, US); Nova Rodovia Andaraí/Mucugê, a 15–20 km ao S de Andaraí, S. A. Mori & F. P. Benton 13119 (A, NY). **Espírito Santo:** Reserva Florestal da CVRD, Linhares Esp. Santo Est. Flamengo, ant. x-1, Km 4232, lado esquerdo, G. L. Farias 50 (A); Reserva Florestal da CVRD, Linhares, P. Sapo, ant. 161, Km 0.06, lado esquerdo, D. A. Folli 73/79 (A). **Goiás:** Serra dos Cristais, 5 km by rd. of Cristalina, W. R. Anderson et al. 8162 (A, NY); Serra Dourada, ca. 15 km (straight line) S of Goiás Velho, W. R. Anderson et al. 10048 (A, AAU, MO, NY, US); 26–31 km S of Goiânia along Hwy. BR-153, G. T. Davidse et al. 12260 (AAU, NY, PMA, US); Contraforte Central, ca. 24 km NE of Catalão, H. S. Irwin et al. 25385 (F, MO, NY, US); Serra Geral do Paraná, 20 km S of São João de Aliança, H. S. Irwin et al. 32102 (A, MO, NY); Caiapônia, 9 km S, P. I. Oliveira 401 (GB); W of Filadelfia on Serra de Mamoneira, G. T. Prance & N. T. Silva 58521 (A, F, NY, US); 35 km S of Caiapônia, Serra do Caiapó, G. T. Prance & N. T. Silva 5968 (A, F, NY, US); entre Jataí Caiapônia, ca. 123 km de Jataí, em frente a serra de Caiapó, 2 Oct. 1968, Sidney & Onishi 1023 (A [2]); Meia Ponte, E. Ule s.n. (R). **Maranhão:** Ilha de Balsas, region betw. Balsas & Parnaíba rivers, 13 km SSE of Loreto, G. Eiten & L. T. Eiten 10803 (K, NY, US); a 2 leugas de Carolina, J. M. Pires & G. A. Black 1607a (US). **Mato Grosso:** estr. Santarém–Cuiabá,

BR 163, Km 762, 30 km de Guarantan, Serra de Cachimbo, *I. L. Amaral et al.* 823 (A, MO, NY); 25 km S of Xavantina, *H. S. Irwin et al.* 17086 (F, GH, MO, NY, US); 70 km S of Xavantina, *H. S. Irwin et al.* 17452 (F, GH, MO, NY, US); 0.5 km SE of base camp, *D. Philcox et al.* 3351 (K, MO, NY); Sararé, *J. M. Pires & M. R. Santos* 16402 (F, GH, MO, NY). **Minas Gerais:** Serra do Espinhaço at Lapinha, ca. 19 km N of Sêro on rd. to Diamantina, *H. S. Irwin et al.* 20808 (F, G, NY); 33 km SW of Diamantina, near Gouveia, *H. S. Irwin et al.* 22289 (F, K, NY); alrededor de Itapanhoacanga, base de la Serra do Espinhaco, *M. M. Mello-Silva et al.* 4322 (CTES); 30 km de Felixlandia para Brasília, *J. M. Pires* 57974 (A, MO, NY); Caratinga, Estação Biol. caratinga, *K. B. Stier* 697 (A, NY). **Pernambuco:** Rio Petro, 1 Jan. 1838, *C. A. Gardner* 2941 (K). **BOLIVIA.** **Santa Cruz:** Parque Nacional Noel Kempff Mercado, ca. camp. viejo de los Fierros, 3–5 km N del camino principal entre Los Fierros y Tarbo, sobre el camnio a la meseta, *M. S. Arroyo* 2829 (CTES); camp. Toledo, a 100 m al E de la casa, yendo hacia el río Paragúa, *R. Guillén & V. Choré* 1872 (NY, USZ); Parque Nacional Noel Kempff Mercado, Los Fierros, 5–8 km al NE de la carretera, *T. Killen et al.* 5642 (NY, USZ); Reserva Ecologica El Refugio, a 10 km hacia Los Fierros, *T. Killen et al.* 6725 (MO); Estación Flor de Oro, W side of Río Guaporé [Río Iténez], 0–1 km W of airstrip, *M. Nee* 41218 (GH, LBP, NY); 3 km NW of buildings at Estación Oro, along oxbow lake along Río Iténez [Río Guaporé], *M. Nee* 41458 (GH, NY); Estación Flor de Oro, margen del Río Iténez (Guaporé), frontera con Rondonia, 20 km N de Serranía de Huanchaca, 85 km E del Río Paragua, *M. Peña & R. Foster* 172 (F, MO, NY); Serranía de Huanchaca, Parque Nacional Noel Kempff Mercado, 5–7 km al S del Río Itenes o Guaporé, 15 km SE del Estación de Flor, *M. Toledo* 50 (F, USZ).

4. *Emmotum orbiculatum* (Benth.) Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 178. 1852. Basionym: *Pogopetalum orbiculatum* Benth., Proc. Linn. Soc. London 1(10): 88. 1841. TYPE: Guyana. Dry savannahs on Padawire River, s.d., *R. Schomburgk s.n.* (holotype, K!).

Emmotum holosericeum Ducke, Arch. Inst. Biol. Veg. 4: 45. 1938. TYPE: Brazil. Amazonas: Borba, Rio Madeira, *A. Ducke* 35548 (holotype, BR!; isotypes, K!, U not seen, US!).

Shrub or trees, 3–12 m. *Leaves* coriaceous, sharply bicolored, light green or yellow on the abaxial surfaces and dark green and shiny on the adaxial surface; lamina 10–22 × 6–13 cm, widely oblongate, widely elliptic, or widely ovate, sericeous or velvet on the abaxial surface, apex mucronate to shortly acuminate, sometimes retuse, base rounded; secondary veins 8 to 9 pairs, conspicuous; petiole 1–2 cm. *Inflorescences* axillary, 1- to 4-floriferous branches, up to 3 cm, sericeous; peduncle up to 1 cm. *Flowers* pentamerous; pedicels up to 3 mm; *calyx* campanulate, sepal lobes ca. 1.5 × 1.5 cm, widely triangular; *corolla* with the petals 4–4.5 × 1–1.2 mm, narrowly oblongate, bearded on the adaxial surface, on the base, and near the apex, rarely continuous or

glabrous; *stamens* 4–4.5 mm, filaments to 2 mm long, swelled; anther 1–1.2 mm, basifixed, connective elliptic, apex slightly prolonged; *pistils* 2–2.5 mm, ovary hirsute, base glabrous; style up to 0.5 mm, centric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum orbiculatum* occurs in Colombia (Vaupés), Guyana, and Brazil (Amazonas and Roraima). It grows in forests at 100 m elevation.

Phenology. *Emmotum orbiculatum* flowers year around and fruits from (March to) May to December.

IUCN Red List category. *Emmotum orbiculatum* is a common species in the Brazilian Amazon Basin. There are numerous botanical collections, including some from inside protected areas. Therefore, this species could be excluded from any category of protection according to IUCN Red List criteria (IUCN, 2001), or alternatively could be listed as Least Concern (LC).

Discussion. *Emmotum orbiculatum* is similar to *E. amazonicum* and *E. nitens* in having the base and apex of the filament dilated, the anthers oblong-linear with the connective elliptic and prolonged, and the ovary with a short style, less than 0.5 mm long. *Emmotum holosericeum*, a species here referred to the synonymy of *E. orbiculatum*, is only known from the type specimens. Ducke (1938) considered the indument characters of this sterile specimen different enough to propose a new species. Here we follow the de Roon (1994) point of view in referring *E. holosericeum* to the synonymy of *E. orbiculatum*, because a similar pubescence pattern has been observed in some other species of this clade, such as *E. nitens*.

Additional specimens examined. **BRAZIL. Amazonas:** Rio Cuieiras, Rio Cuieiras near mouth of rio Branchinho, *A. B. Anderson* 92b (MO, NY), *A. B. Anderson* 178 (MO, NY); Manaus–Caracarái Rd., Km 140, *C. C. Berg et al.* P18177 (A, NY). **Roraima:** entre Km 350 e 355 da Estr. Manaus–Caracarái (BR 174), *C. A. Cid Ferreira* 9068 (F, GH, NY); rodovia perimetral N 20 km E de Caracarái, *J. M. Pires & P. Leites* 14843 (A, INPA); BR 174, Manaus–Venezuelan Hwy., Estr. Manaus–Caracarái, Km 350, N of Rio Branchinho, *W. C. Steward et al.* 80 (A, F, NY, US). **COLOMBIA. Vaupés:** Rio Kuduyari, *H. García Barriga et al.* 15837 (K). **GUYANA.** Rio Padawire, *Schomburg* 231 (K).

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APPENDIX 1. Characters and character states used in the cladistic analysis of *Emmotum*.

- Habit: tree (0), shrub (1).
- Pigment in chemical reaction of the flower in alcohol: absent (0), red (1), black (2).
- Malpighiaceae hairs: present (0), present but arms unequal (1), absent (2).
- Articulated hairs: absent (0), present (1).
- Length of the petiole (cm): 0.4–0.8 (0), 1–2.5 (1).
- Length of the lamina (cm): 2–5 (0), 6–20 (1).
- Form of the apex of the leaves: acute (0), narrowly acute (1), rounded (2).
- Bicolorous leaves: no (0), yes (1).
- Number of pairs of secondary veins: (0) 2 to 3, (1) 5 to 15.
- Patent secondary veins: no (0), yes (1).
- Persistent pubescence of the leaves: no (0), yes (1).
- Number of flower parts: tetramerous (0), pentamerous (1).
- Inflorescence: spike (0), cyme (1), panicle (2).
- Sexuality: unisexual (0), bisexual (1).

15. Number of flowers: 1 to 3 (0), 10 to 20 (1), 50 or more (2).
16. Sepal aestivation: imbricate (0), valvate (1).
17. Flower color: greenish to yellowish (0), white (1).
18. Internal grooves of the petals present: no (0), yes (1).
19. Petal connation: joined at the base (0), free (1).
20. Petal texture: thickened (0), slightly developed (1), membranous (2).
21. Petals with cylindrical hairs on the inner surface: no (0), yes (1).
22. Cylindrical hairs continuous on the inner surface: yes (0), no (1).
23. Shape of the filament: obovate (0), narrowly ovate (1), ovate (2), filiform (3).
24. Length of the filament (mm): absent (0), 1.5–2 (1), 3.5–5 (2).
25. Anthers (attachment): basifixed (0), dorsifixed (1).
26. Anthers (shape): oblong (0), sagittate (1), cordate (2), globose (3).
27. Apex of the filament: attenuated (0), dilated (1), as wide as the middle section (2).
28. Ratio length of the anther and filament: anther is several times longer than the filament, more than 5:1 (0), anther is as long as the filament, 1:1 (1), anther is about half as long as the filament, 1:2 (2), anther is three or four times smaller than the filament, 1:3–4 (3).
29. Connective (shape): very broadly ovate (0), broadly ovate (1), elliptic (2), ovate (3), absent (4).
30. Connective (prolongation): long (0), short (1), absent (2).
31. Ring of tissue around the base of the ovary: no (0), yes (1).
32. Length of the style (mm): absent (0), 0.1–0.5 (1), 2.5–4 (2), 5 or more (3).
33. Style position: central (0), lateral (1).
34. Ovary (type): unilocular (0), multilocular (1).
35. Ovary (pubescence): no (0), yes (1).
36. Fruit (shape): oblong (0), globose (1).
37. Fruit (size, cm): more than 3 (0), less than 1.5 (1).
38. Mesocarp (fleshy): present, very well developed (0), present, tiny (1), absent (2).
39. Fruits (apex): rounded or acute (0), shortly mucronate (1), acute (2).
40. Endocarp (suture): absent (0), present, slightly developed (1), present, very well developed (2).
41. Embryo (size): small (0), big (1).

Comments about the characters and character states:

[2] Pigment in chemical reaction of the flower in alcohol: When flowers and leaves are soaked in 50% alcohol, the liquid turns red or black, or else remains unchanged. Despite the fact that the biochemical nature of these processes is unknown to us (most likely an oxidative phenolic reaction), we considered this coloration as an alternative state of a single chemical character. In *Oecopetalum* and *Ottoschulzia* the pigment remains unchanged (0); in all species of *Poraqueiba* and *Emmotum* it turns red (1); and in *Calatola* the liquid becomes black (2).

[8] Bicolourous leaves: When specimens of Icacinaceae dry, some have bicolorous leaves; this occurs in some taxa of *Emmotum* sect. *Emmotum*, all members of *Emmotum* sect. *Brevistyla*, and some members of the outgroup. It does not occur in *Calatola* (dries completely black), *Oecopetalum* and *Poraqueiba* (dries yellow-brown), and *Ottoschulzia* (dries brown).

[13] Inflorescence: The main inflorescence of the Icacinaceae taxa is a panicle, but in *Calatola* the male inflorescence has flowers without pedicels giving rise to a spike (0); in *Ottoschulzia* and *Oecopetalum* the inflorescence has a terminal flower giving rise to a cyme (1), with few flowers in the first genus and many flowers in *Oecopetalum* (see character 15 below). In *Poraqueiba* and *Emmotum* the inflorescence is the generalized panicle of the family (2).

[14] Sexuality of flowers: The Neotropical genera of Icacinaceae are mainly monoecious plants with bisexual flowers (1), but *Calatola* has dioecious and unisexual flowers (0).

[15] Number of flowers: The number of flowers per inflorescence is variable among genera. In *Ottoschulzia* the inflorescence is reduced to one to three flowers (0); in *Emmotum* and *Poraqueiba* the number of flowers per inflorescence varies from 10 to 20 (1), but in *Calatola* and *Oecopetalum* it increases to more than 50.

[18] Internal grooves of the petals present: The petal of some of these taxa has the abaxial surface with special kinds of structures. We reduce this morphological complex character to a binary situation. In *Ottoschulzia*, *Oecopetalum*, and *Poraqueiba* there is a very well-developed internal groove (1), while in *Calatola* and *Emmotum* the internal surface of the petals lacks any kind of appendages (0).

[21] Cylindrical hairs on the inner surface of the petals: The typical indument in the inner petal face of *Emmotum* is due to the presence of cylindrical hairs (1), but in all taxa of the outgroup this indument is absent or made up of other kinds of ornamentation (0).

[22] Cylindrical hairs continuous: This character does not apply to all members of the family, only to members of the genus *Emmotum* (see character 21, above). In *Emmotum* two types of indument can be observed on the inner face of the petal. In members of *Emmotum* sect. *Emmotum* the indument is dense and continuous from the base to the apex (0), while in members of *Emmotum* sect. *Brevistyla* the indument is reduced to two tufts of hairs on the base and the apex (1). For the outgroup, the character was recorded as not applicable (?).

[23] Shape of the filament: The outline of the filament is variable between genera of the Icacinaceae family. In *Poraqueiba* it is massive, fleshy, thick, and obovate (0); in *Oecopetalum* and *Ottoschulzia* it is slightly fleshy, thick, and narrowly ovate (1); in *Emmotum* it is slightly thickened and ovate (2), and in *Calatola* it is filiform (3).

[24] Length of the filament (mm): This continuous character can be scored in three discrete states; in *Calatola* the filament is almost absent (0); in members of *Emmotum* sect. *Brevistyla* it is medium sized and 1.5–2 mm long (1); and in members of *Emmotum* sect. *Emmotum*, *Oecopetalum*, and *Ottoschulzia* it is 3.5–5 mm long (2).

[26] Anthers (shape): The outline of the anther is variable in *Emmotum* and other members of the outgroup. In *Poraqueiba* the anther is oblong (0), sagittate in *Oecopetalum* and *Ottoschulzia* (1), cordate in *Emmotum* (2), and globose in *Calatola* (3).

[27] Apex of the filament: The apex of the filament is variable within *Emmotum* and members of the outgroup. This character is better understood if we describe the apex as compared with the middle portion of the filament. Thus, in *Poraqueiba* and in members of *Emmotum* sect. *Brevistyla* the apex is attenuated, narrower than the middle section (0), in *Emmotum* sect. *Brevistyla* the apex is dilated, much broader than the middle section (1), and in *Calatola* it is as wide as the middle section (2).

[28] Ratio of anther length:filament length: There is a significant difference between the size of the filament and anther, and these differences can be expressed in relation to its proportion. In *Calatola* the anther is several times longer than the filament, more than 5:1 (0). In members of *Emmotum* sect. *Brevistyla*, the anther is as long as the filament and the ratio is 1:1 (1). In *Poraqueiba* the anther is about half as long as the filament, with a ratio of 1:2 (2). In members of *Emmotum* sect. *Emmotum*, *Oecopetalum*, and *Ottoschulzia*, the anther is three or four times smaller than the filament, 1:3–4 (3).

[29] Connective shape: There are important differences in the shape of the connective. In *Poraqueiba* it is very broadly ovate (0), in *Oecopetalum* and *Ottoschulzia* it can be defined as broadly ovate (1), in members of *Emmotum* sect. *Brevistyla* it is elliptic (2), in members of *Emmotum* sect. *Emmotum* it is ovate (3), and in *Calatola* it is absent (4).

[30] Connective (prolongation): In general the apex of the connective does not extend to the anther, but it is massive and long in *Poraqueiba* (0), short in members of *Emmotum* sect.

Brevistyla (1), and absent in members of *Emmotum* sect. *Emmotum*, *Oecopetalum*, *Ottoschulzia*, and *Calatola* (2).

[31] Ring of tissue around the base of the ovary: In general in all members of *Emmotum* and the outgroup there is no difference in the base around the ovary (0), but in two species, *E. acuminatum* and *E. floribundum*, there is a diminute ring of tissue surrounding the base of the ovary (1).

[32] Length of the style (mm): The length of the style is variable in members of *Emmotum* and the outgroup, and it is particularly important in members of *Emmotum*. In *Calatola*, the style is absent (0); in members of *Poraqueiba* and *Emmotum* sect. *Brevistyla* the style is short, less than 0.5 mm long or smaller than the ovary (1); in members of *Emmotum* sect. *Emmotum* the style is long, 2.5–4 mm or twice as long as the ovary (2); in *Oecopetalum* and *Ottoschulzia* the style is longer, ca. 5 mm (3).

[33] Style position: In general, in all members of *Emmotum* and the outgroup the style is central (0), but in two species of *Emmotum*, *E. acuminatum* and *E. floribundum*, the style is displaced somewhat sideways, becoming eccentric or lateral (1).